Distribution and Zoogeography of the Bivalvia of the Eastern Pacific Ocean

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Abstract

BERNARD, F.R., S.M. MCKINNELL, AND G.S. JAMIESON. 1991. Distribution and zoogeography of the Bivalvia of the eastern Pacific Ocean. Can. Spec. Publ. Fish. Aquat. Sci. 112: 60 p.

The incidence of existing marine bivalve fauna by latitude and depth is recorded for the Eastern Pacific Ocean and offshore islands. Hypotheses concerning long and short term factors influencing the coast-wide distribution of the bivalve fauna are formulated and examined. Consideration is given to global effects of plate tectonics, continental displacement and environmental factors. The number and diversity of bivalve species increases with decreasing latitude. The relative mean palaeontological age of living bivalves as a function of latitude suggests that age increases from north to south. There is evidence that mean paleontological age is greater for intertidal bivalve species than for deeper-water representatives and there is no indication that older taxa are more widely dispersed. Species number at latitude is directly correlated with mean ocean temperature for both intertidal and subtidal bivalves. Mean tidal cycle and area of continental shelf available for settlement are not well correlated with the number of species present at latitude. There is some indication that species at higher latitudes, irrespective of bathymetric range, have extended ranges through submergence to cooler depths with decreasing latitude.

Ordination and clustering techniques are used to examine the size and distribution of zoogeographic provinces. Provincial boundaries are presented and the characteristics of these provinces are described. Finally the bivalve fauna of the Eastern Pacific islands are examined and discussed. Unlike the Hawaiian Archipelago and the Isla de Pascua, these islands all show a strong or exclusive West American component with little contribution from the Indo-Pacific.

Résumé

BERNARD, F.R., S.M. MCKINNELL, AND G.S. JAMIESON. 1991. Distribution and zoogeography of the Bivalvia of the eastern Pacific Ocean. Can. Spec. Publ. Fish. Aquat. Sci. 112: 60 p.

Nous avons établi, selon la latitude et la profondeur, la fréquence des bivalves de l'est du Pacifique et des îles océaniques de cette région. Des hypothèses concernant les phénomènes qui se manifestent sur de courtes ou sur de longues périodes et qui agissent sur la distribution des bivalves sur toute la côte est de l'océan Pacifique sont avancées et examinées. Nous avons considéré les effets à grande échelle de la tectonique des plaques, du déplacement continental et des facteurs environnementaux. Il en est ressortit que l'abondance et la diversité des bivalves varient en raison inverse de la latitude. De plus, l'âge paléontologique relatif moyen des bivalves actuels va en augmentant du nord au sud. Aussi, des données montrent que l'âge paléontologique moyen des bivalves intertidaux est supérieur à celui des bivalves vivant à de plus grandes profondeurs. En outre, rien ne semble indiquer que les taxons les plus anciens ont une distribution géographique plus étendue. Le nombre d'espèces selon la latitude est corrélé directement avec la température moyenne de l'océan. Par ailleurs, à une latitude donnée, le régime moyen des marées et la superficie du plateau continental propice à l'établissement des bivalves intertidaux et infratidaux ne sont que faiblement corrélés avec le nombre d'espèces présentes aux différentes latitudes. Selon certaines données, les espèces des hautes latitudes, peu importe les profondeurs auxquelles elles vivent, ont des aires de distribution étendues grâce à leur établissement dans les eaux plus profondes et plus froides des latitudes inférieures.

Des méthodes d'ordination et d'analyse en grappes ont permis de lacaliser les régions zoogéographiques et de déterminer leurs dimensions. Cette étude donne les limites et les caractéristiques de ces régions. Enfin, nous analysons la faune des îles de l'est du Pacifique. Contrairement aux faunes de l'archipel d'Hawaii et de l'île de Pâques, cette faune ressemble beaucoup ou est identique à celle de l'ouest de l'Amérique tandis qu'elle a peu d'affinités avec celle de la région Indo-Pacifique.

Introduction

The nearly continuous and general north-to-south trending Pacific coastlines of North and South America cross all the major global marine climatic zones and include many biotopes. With exception of the localized accretion of land extending the shoreline westward, these coasts have persisted largely unchanged since they formed the western edge of the supercontinent Pangaea, more than 250 × 10^6 y.b.p. (years before present). The Pacific Ocean is the largest and oldest ocean basin, presently accounting for approximately half of the earth's ocean surface. These factors permitted more time for establishment and diversification of the marine biota than that available in the Atlantic Ocean, a basin formed by separation of North and South America from Eurasia and Africa. Faunal mixing with the adjacent Indo-Pacific regions is limited by the intervening wide Pacific Ocean and exchange via the Arctic Ocean has been sporadic. Migration through the Antarctic regions has been restricted by the long-prevailing oceanic circulation and great distances to land. The formation of the Isthmus of Panama approximately 1.5 to 3 × 10^6 y.b.p. completed the isolation of the Eastern Pacific faunal region.

Consistent differences in the composition of faunal assemblages inhabiting comparable geographic regions led to the concept of biogeography and the discipline of chorology, which examines spatial relationships of organisms (Beklemishev 1982). The presence of a particular species at a location is due either because it originated there, or migration from elsewhere. Faunal diversity is either endogenous or exogenous in origin. To this simple concept must be added the role of continental drift, i.e. the rafting on tectonic plates of entire biomes to new locations. Distribution, in the short term, is the combined consequences of individual specific tolerance to environmental regimes, availability of habitat niche, competitive exclusion, and the effectiveness of abiotic barriers to migration. In the long term, faunal differences are the consequences of all the factors mentioned, together with the speciation history of the organism and the transportive action of plate tectonics. Ultimately, evolutionary plasticity, expressed as the phylogeny, sets the underlying signature of distribution that is then modified by other causes. Dearth of detailed phylogenetic information renders the majority of distributional hypotheses speculative. However, marine biogeography is still in the descriptive stage and more distributional data, based on refined taxonomy, are required before general hypotheses can be proposed.

While it is not likely that universal zoogeographic patterns are discernible based on a limited sample of a few taxonomic groups, it is reasonable to expect progress from analysis of the distribution of a single family (Schilder 1965), either on a global basis, or in a major region. Such studies, undertaken independently on several groups, may eventually be amalgamated and compared.

Marine zoogeographic studies known to us are based on faunal inventories without reference to abundance or biomass and there exists no quantitative definition of provincialism or biogeography. The pioneer marine biogeographers established faunal boundaries on the general knowledge of distribution, together with subjective interpretation of oceanographic discontinuities reported by mariners. In spite of the advent of computers, stringent mathematical analysis and clustering techniques, this essentially subjective approach to biogeography has continued. The more recent work, characterized by progressively finer divisions and proposal of unwarranted units even at the province level, requires revision. Application of computer technology allows manipulation of large data sets, but it is critically important that ecological information be incorporated. It is unlikely that analyses based on mixed taxa, with wide variations in adaptative tolerance and life-styles, can effectively identify faunal boundaries. For example, it is improbable that the benthos opposed to nekton, or invertebrates compared to vertebrates, share fundamentally similar distribution patterns. While there is a general response by all organisms to oceanographic discontinuities, clear-cut universal faunal boundaries are not general, except at the few locations of profound and overwhelming oceanographic change. This problem may be overstated, as it is recognized that biogeographic boundaries are usually regions of overlap and gradual faunal replacement (Schenck and Keen 1936).

The first objective study of geographical distribution utilized the frequency of the arithmetic means of latitudinal range of molluscs of the Northeastern Pacific Ocean (Schenck and Keen 1936; Schenck 1937). It is now accepted that distributional end-points are more significant than the clustering of mid-points, but this fundamental work influenced the development of marine biogeography. End-point analysis was used by Newell (1948) when reworking the data of Schenck and Keen and in the initial computer analysis of these data (Valentine 1966).

Molluscs have figured prominently in many early marine biogeographical studies, and gave rise to vigorous discussion (e.g. Petit de la Saussaye 1858; Fischer 1858; Lamy 1933). The class Bivalvia is particularly useful as it is well represented in the majority of benthic communities. The virtually sedentary adult life and the planktonic larval stage of many bivalves make them good environmental indices. Bivalves are well represented as fossils since at least the Early Ordovician (Pojeta 1971), and the evolutionary conservatism of the entire class permits paleobiogeographic assumptions based on the belief that similar shell morphology in extinct species indicate a life-style at least comparable to that of living representatives.

Except for some early general and essentially speculative reviews, biogeographic studies dealing with the eastern Pacific Ocean have been of limited regional focus and predominantly concerned with the North Pacific region (Carpenter 1857). Hayden and Dolan (1976) attempted an analysis on a hemispheric scale using a small number of shallow water invertebrates and compared their distribution to coastal marine climates and wave regimes. We review distribution of the marine bivalve fauna of the eastern Pacific Ocean from Bering Strait, Alaska (66°N), to south of Cabo Hornos (Cape Horn), Chile (60°S) (Fig. 1), based on the catalogue of Bernard (1983) and reworking of some new records of the

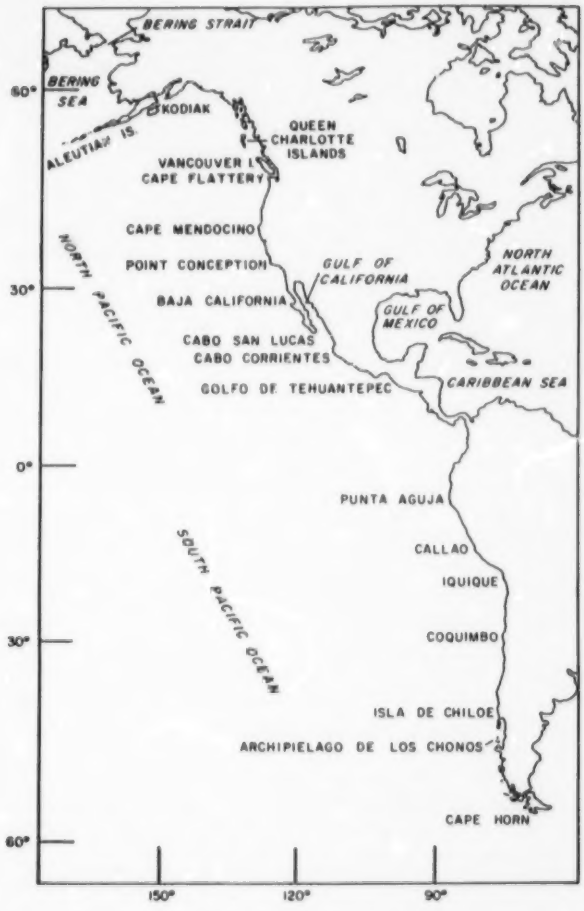

FIG. 1. The eastern Pacific Ocean showing the location of mainland place names used in the text.

Galapagos and Hawaiian Islands fauna. Our approach is chorological in the sense of narrative biogeography (Ball 1976), though we attempt to speculate on the principal causative mechanisms. We do not discuss the role of epicontinental seas which at times occupied significant portions of Gondwana (Loczy 1971) and other continents. These may have exerted a significant influence on the regionality of western North America, but have decreased since the Mesozoic. We follow the current interpretation of continental displacement during the last quarter million years, but do not consider the possibility of global expansion (Owen 1976). This may have important implications for the biogeography of the eastern Tethys Sea, but would have little effect on the eastern Pacific region. We recognize that the recently proposed hypothesis of displacement of the geographic poles (Andrews 1985) may have had a profound influence on the faunal regionality of the North Pacific Ocean.

Methods

This paper is based on a catalogue of the living bivalve molluscs of the eastern Pacific Ocean (Bernard 1983) and additional information on the insular islands, the Hawaiian Archipelago, and Isla de Pascua derived from study of new material and recent collecting. The original records were consulted and actual distribution noted, rather than the end-points cited in the catalogue. Preliminary analyses along selected bathymetric gradients suggested eight significant depth categories (Intertidal, subtidal–100, 100–500, 500–1000, 1000–2000, 2000–3000, 3000–4000, 4000+ m). Due to the very few records in the last three catagories, analysis was limited to the five shallower groups; however, general speculations on abyssal distribution are made.

Input Data

A coding form was prepared to represent the coastline north of the Bering Strait and several degrees south of Cabo de Hornos. This transect was divided into one degree latitude blocks. To cover all the depth categories and the inserts for the oceanic islands and the area of "overlap" represented by the Gulf of California, 724 blocks were required. A potential difficulty involved the Aleutian Archipelago, the sole extensive longitudinal component of the western coastline of America. The compression into a few latitudinal blocks of the east to west sweep of islands aggregates distributional information. As few bivalves have end-points of distribution at the Aleutian Islands, no compression artifact was anticipated. A separate analysis of the Aleutian bivalve fauna showed it to be essentially uniform from the Alaskan Peninsula (158°W) to Adak Island (177°W). A similar problem exists when comparing latitudinal clines of diversity, due to the variable width of the continental shelf, so that a simple area effect may be confounded as a latitudinal phenomenon. To overcome this objection, analyses of regionality include an area factor.

The zone of overlap represented by the Gulf of California where the tropical fauna penetrates northwards relative to that present on the west side of the peninsula of Baja California, is accommodated by assigning two sets of latitudinal blocks, one for the inner, Gulf area, and the other for the outer oceanic shelf. No other regions of extensive faunal displacement were identified, though some localised differences were present between the mainland coast and major continental shelf islands (Vancouver Island, Chiloe Island). Small-scale differences, such as those between exposed headlands and protected bays, and regions of oceanic upwelling, are masked by the size of the blocks utilized, but are discussed and considered in the text.

The distribution of each species was rounded to the nearest one degree of latitude and scored in the appropriate latitude and depth box. In some cases the intervening boxes between the distribution end-points were also occupied, but in the majority of cases distribution was discontinuous. This may represent the true pattern of distribution, or merely reflect inadequate collecting coverage. The scoring of the latitudinal boxes for each species resulted in a presence or absence matrix. The occurrence of a species in other areas of the world was recorded, as well as the palaeontological range in western America. These data were digitised and analysed using computer techniques.

Analyses to determine provincialism were made initially using all depth zones combined with the presence/absence of 1229 bivalve species over the entire west coast and north of South America. Offshore island faunas were excluded and no assumption concerning continuity of species distribution between bathymetric end-points was made.

Possible bathymetric differences were examined by segregating the presence/absence matrices into five depth categories (Intertidal, subtidal — 100, 100–500, 500–1000, 1000–2000 m). Analyses were run on the five data sets and compared with the combined data for significant differences.

Analytical Techniques

The BMDP program 1M was used to compute similarity between latitude blocks based on species presence/absence. The measure of similarity used to cluster the blocks was the acute angle corresponding to the absolute value of the arccosine of the correlation-option ABSANG in program 1M. Output was in the form of a shaded correlation matrix sorted in the same order as dendrogram output. The BMDP program KM (K-means clustering) was also used to corroborate the result of 1M.

Provincial boundaries were determined by visual inspection of the raw data plots and of calculated correlation matrices. The calculated boundaries were corroborated with species end-point distributions and with other analytical methods such as principal coordinates and K-means clustering.

Terminology

Some of the terms we utilize differ from those in other studies and in other cases terminology has remained undefined. The terms we use are defined as follows:

Eastern Pacific Ocean: The eastern segment of the Pacific Ocean contiguous with the coast of North and South America to approximately 1500 km offshore.

Indo-Pacific Ocean: The Indian Ocean and western Pacific extending eastwards to Isla de Pascua (Easter Island) and a line north to the Hawaiian Archipelago.

Eastern Pacific Oceanic Islands: Offshore islands of the eastern Pacific Ocean less than 1000 km from the American continent and chiefly associated faunistically with the Americas.

Though significant advances have occurred in marine biogeography, there still exists no general terminology based either on conceptual or historical priority (Golikov 1982). Biogeographical terminology should at least distinguish between spatial description and the possible causative factors, but comprehensive terminology attempting to cover both simultaneously is not possible or desirable. The difficulty is illustrated by the prevailing confusion between global latitudinal zonation patterns and biogeographic units. This may not only merge distinct faunas into large latitudinal units, or conversely, needlessly fragment diversity clines, but it furnishes a circular argument to distinguish faunal boundaries (Semenov 1982). Unsatisfactory adaptations of physiological nomenclature have also been attempted. Organisms confined to a single temperature zone have been termed "stenothermal" (e.g. Menzies et al. 1973), or "stenotypic" (e.g. Taylor 1977), yet physiologically these organisms may be markedly eurythermal. Similar difficulties arise from the adaptations of climate terminology (Dall 1921) or various combinations of several factors (Hall 1964).

The terminology we utilize for biogeographic units is not hierarchical, in the sense that lower units do not combine to form higher order units. Although our approach is idiosyncratic and no universal principles are identified, we do recognize the convenience of gathering units with supposed common origins or long association into identifiable common groups (Fig. 2).

Domain: A major artificial grouping composed of disparate marine zoogeographic units, usually associated with one lithospheric plate. It includes units that have a long common history, but may be unrelated faunally.

Province: A biogeographical unit with a commonly descended fauna, demonstrating a degree of homogeneity. The province is the largest definable unit using objective mathematical analysis.

Subprovince: A region of a province demonstrating sufficient faunal differences to warrant separation. In spite of sophisticated mathematical procedures, the subprovince is not an objective entity and depends on the author's bias for identification.

Component: A fauna sharing similar habitat niches and trophic relationships, though constituting species may be different. It includes the concepts of community and biotope (Beklemishev 1982).

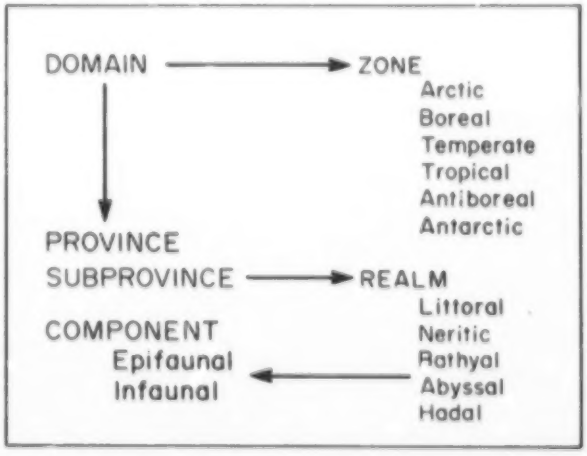

FIG. 2. Relationships of marine benthic biogeographic terminology.

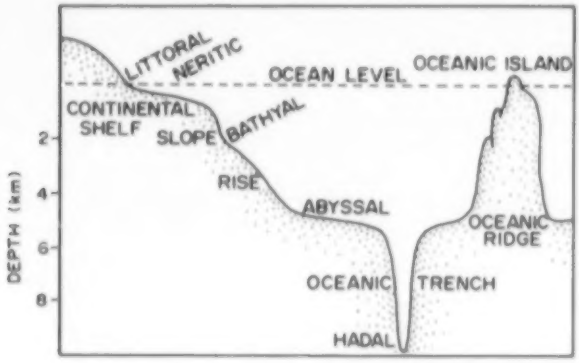

FIG. 3. Oceanic topographic realms.

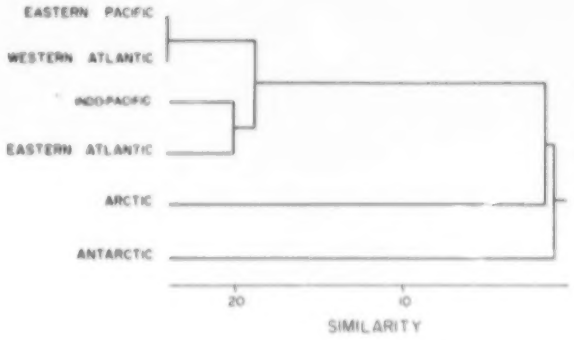

FIG. 4. Dendrogram showing the relationship of global domains based on absolute counts of the genera of living Bivalvia in each domain.

Realm: Topographically dictated component of a province or subprovince. While realms demonstrate marked general similarity of faunas, the constituent organisms may have originated from adjacent provinces. The exception is the Hadal Realm, which appears unconnected to the province, and may be treated as a separate Domain (Fig. 3).

Zone: The zone is not coupled to the province, but may strongly influence biogeography. It is the global marine climate zone, equivalent to the latitudinal climate zone of Ekman (1953) and its variant the "littoral Province" of Hedgpeth (1957). The Zone contains diverse faunas forming distinct, but equivalent communities.

Results and Discussion

We combine interpretation of the distributional data with discussion of the relevant literature. This is followed by a reworking of the provincial segregation of the bivalve fauna. We preface this section with some general comments on the relationship of the Eastern Pacific Domain to other global marine domains.

Global Domains

Marine biogeography on a global scale is speculative and uncertain. Based on the distribution of more than 800 genera of living bivalves, it is possible to recognize five global domains that in general conform to the terrestrial biogeographic zones. The Western Atlantic Domain represents the Nearctic and Neotropical regions, while the Eastern Atlantic Domain is associated with the Ethiopean and Palearctic regions. The matrix of the total number of genera in each domain and their co-occurrences (Table 1) may be analysed using a relative, rather than absolute approach (Webb 1950); this may remove some of the bias due to few fauna present in the Arctic and Antarctic regions. A dendrogram (Fig. 4) based on these calculations associates and removes the polar regions, due to small total population and because nearly 50% of the genera are shared. Faunal similarities between the poles have long been recognized and were discussed by Darwin (1859), and the argument was reviewed by Fischer (1881) who believed the two faunas arose independently. No species are bipolar, with the possible exception of the subpolar *Lasaea petitiana* (Récluz, 1843). This was initially noted by Pelseneer (1903) but is a species widely transported by human agency. We have already stressed the artificiality of the Domain concept; however, distribution of many neritic groups, particularly at generic and higher taxonomic level, correspond well with the major lithospheric plates (Fig. 5).

TABLE 1. Number of living genera of marine Bivalvia and their co-occurrence in global domains.

	E.P.	I.-P.	Arc.	W.A.	E.A.	Ant.
Eastern Pacific	391					
Indo-Pacific	177	459				
Arctic	20	16	23			
Western Atlantic	226	143	20	277		
Eastern Atlantic	194	198	19	187	353	
Antarctic	14	19	10	17	16	35

A clear understanding of relationships is possible based on the distribution of species, but the present state of systematics does not permit an accurate listing of the Indo-Pacific fauna. Analysis of co-occurrences of circumboreal bivalve species, sampled north of 40°N and including the Arctic fauna north of 60°N and from Hudson's Bay, results in a clearer view of relationships (Table 2). This shows that regions where faunal exchange has been active demonstrate significant commonality between adjacent domains (Fig. 6). The Arctic Ocean is an area of exchange that merges all the boreal faunas and cannot be considered a separate domain, but merely a zone of faunal mixing with, at the most, provincial status. The Protoarctic Basin was established by the Cretaceous ($\approx 103 \times 10^6$ y.b.p.) (Herron et al. 1974) and was faunally isolated by the Late Cretaceous approximately 100×10^6 y.b.p. (Churkin and Trexler 1981), so that a largely endemic fauna was developed by the Early Tertiary (Marincovich et al. 1983; Marincovich et al.

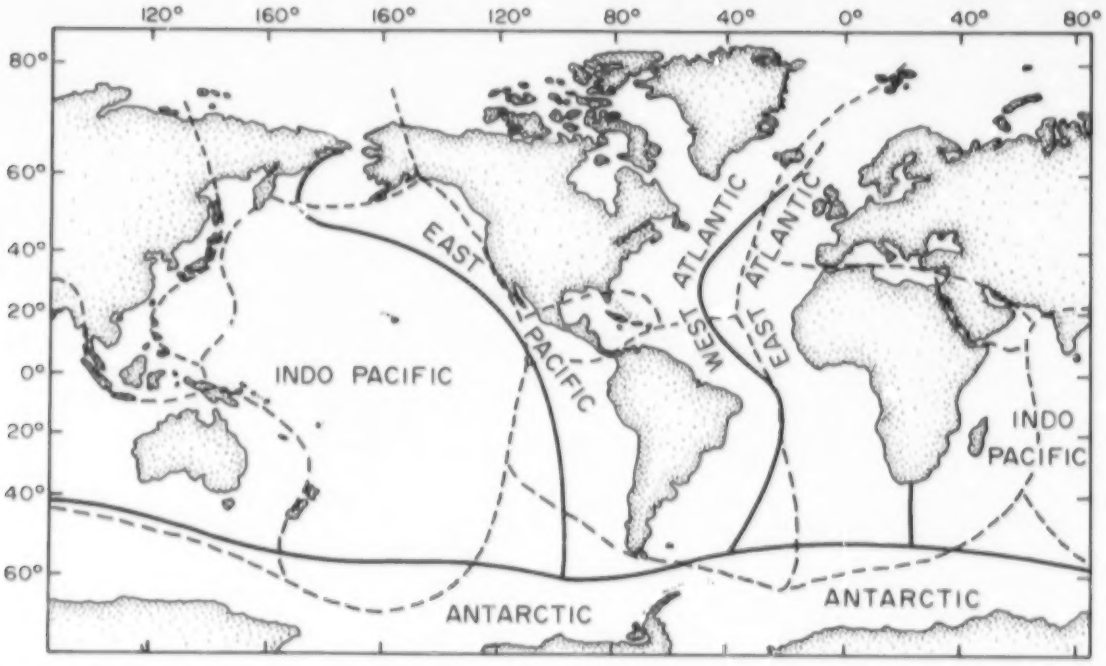

FIG. 5. Global domains, based on the distributions of living genera of marine Bivalvia, and the major lithospheric plates of the world. Margins of lithospheric plates (*broken line*). Margins of global domains (*continuous line*).

TABLE 2. Number of living species of marine Bivalvia and their co-occurrence in global domains north of 40° N latitude.

	Arc.	E.P.	W.P.	E.A.	W.A.
Arctic	90				
Eastern Pacific	51	290			
Western Pacific	17	83	235		
Eastern Atlantic	23	26	2	185	
Western Atlantic	42	31	5	38	191

1985). Connection with the Pacific Ocean was not re-established until approximately 3×10^6 y.b.p. (Hopkins and Marincovich 1984). This fauna, with the possible exception of a small remnant in the deepest basins, was destroyed by successive periods of glaciation. As conditions ameliorated during interglacial epochs, bivalves and other neritic biota from the adjacent boreal regions colonized through the newly opened Bering Strait and across the shallow Greenland and Norwegian Sea. In sharp contrast, the bivalve fauna present in the Antarctic region is strongly differentiated, and below the reach of scouring ice is particularly rich and diverse. It includes numerous endemic species and relics of temperate origin such as the scallop *Admussium colbecki* (E.A. Smith, 1902), and the clams *Laternula elliptica* (King & Broderip, 1831) and *Thracia meridionalis* E.A. Smith, 1885. The Antarctic fauna requires more research, but based on the list of Powell (1960) and reviews by Dell (1964), Nicol (1966) and other contributions, a case can be made to consider the Antarctic a distinct Domain.

The extensive Indo-Pacific Domain is the region that has experienced the least environmental perturbation since the fragmentation of Pangaea and may be considered the oldest faunal region. Its high diversity has long been recognized (Buonanni 1681) and comprises the most diverse bivalve fauna, including numerous endemic taxa at the genus and family levels. A characteristic is the wide geographic distribution of many of the species (Springer 1982; Kohn 1983) which demonstrate only minor

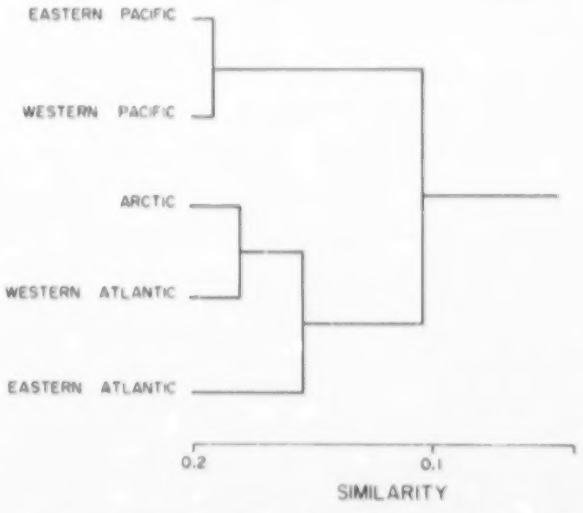

FIG. 6. Dendrogram showing the relationship of circumboreal global domains based on absolute counts of the species of living Bivalvia in each domain.

morphological plasticity despite the isolation of some populations, though biogeographic units are discernable (Powell 1957). Few of the bivalves have penetrated into the Eastern Pacific Domain (Hertlein 1937; Emerson 1978; Vermeij 1978). This strong containment to the east is in contrast to the large numbers of bivalves extending westward to the Indian Ocean, the shores of East Africa and into the Red Sea.

The Eastern Pacific Domain is well demarcated and represents an ancient region that has undergone relatively little tectonic displacement. Two centres of faunal intrusion may be identified, one through the Gulf of Alaska from the Asiatic segment of the North Pacific Ocean and the Arctic Ocean, and the other from the Caribbean via the incompleted Isthmus of Panama. The occurrence of some organisms with low dispersive potential, such as the hermatypic corals, are relics of the Tethyan fauna in the Eastern Pacific (Heck and McCoy 1978).

Atlantic Ocean and Mediterranean Sea

The Atlantic Ocean occupies the expanding rift separating North and South America from Eurasia and Africa. During the Jurassic ($\approx 180 \times 10^6$ y.b.p.), numerous North Atlantic marine invertebrates were common to the neritic zones of Europe and North America (Hallam 1965), as would be expected of a young and expanding oceanic basin. The separation of Eurasia from North America during the Cretaceous ($\approx 100 \times 10^6$ y.b.p.) led to faunal isolation of the east and west sides and a distinct North American Atlantic neritic fauna became established (Imlay 1965). Numerous bivalve groups migrated from the Pacific Ocean through the Arctic Ocean to colonize the shelf of northeastern America during the Tertiary (Gerth 1925) and set a common stamp on the northern areas of both the Eastern and Western Atlantic Domains.

We include the Mediterranean Sea in the Eastern Atlantic Domain as the contemporary bivalve fauna is derived by colonization of Atlantic elements. In the Early Miocene ($\approx 15 \times 10^6$ y.b.p.), the Protomediterranean fauna was entirely Tethyan. Coalescence of the African and Eurasian landmasses separated it from the Indian Ocean. The western end was also occluded, converting the Mediterranean Sea into a series of drying salt lakes and deserts (Hsu 1984) that persisted until the Pliocene ($\approx 6 \times 10^6$ y.b.p.) and totally extirpated the marine fauna. The opening of the Strait of Gibraltar created a new inland sea that was colonized by Atlantic biota.

Plate Tectonics and Marine Biogeography

The general conformation of global faunal domains to the major lithospheric plates provides strong circumstantial evidence for the significant role of continental drift in the development of contemporary regionality. That is, geographical distribution of organisms and geography evolved together (Croizat 1958). In this sense, all modern zoogeography is vicariance biogeography (the vicariography *sensu* Springer 1982). While the concept of the role of changing geography is central to contemporary biogeographical thought, it is not a new idea as Ihering (1907) noted its possible significance, but it required the theory of plate tectonics to permit its full development.

The continents have undergone a long and complex history of changing relationships, coalition and separation as they drifted under the influence of movement of the lithospheric plates. These relationships significantly influenced regionality, either directly by the rafting of entire biomes to new regions, or indirectly by the formation of barriers to distribution (Valentine 1971) and the profound alteration of oceanographic regimes (Meyerhoff 1970). Further pressure on the fauna arose from the general alteration of climate resulting from changed relationships between the land and sea surface. In the contemporary situation of high continentality, the increased environmental heterogeneity could also contribute significantly to the formation of distinct biogeographic units (Valentine and Moores 1972). As there are significant differences between contemporary and ancient biogeographic patterns (Campbell and Valentine 1977), it may be concluded that the changing relationship and number of continents gathered the participating faunal elements, while environmental interaction together with biological competition, selected the fauna that ultimately formed contemporary biogeographic units.

The migration and translocation of species appears to be a potent stimulator of evolutionary change, as it is seldom completed at the place of species origin. Displacement and mixing of various faunal elements together with their ongoing speciation pattern results in non-synchroneity of spatial distribution (Xu 1985). The persistence of pockets of relic populations in protected regions has been termed geographical heterochrony (Petuch 1982).

Interaction of the lithospheric plate boundaries altered the structural relationships of the coastline and continental slope. However, the American Cordillera, a complex of mountains and plateaus extending from Alaska to Patagonia remained the dominant feature since at least 300×10^6 y.b.p. Convergence of oceanic plates created volcanic terrains that subsequently remained as oceanic islands and seamounts, or accreted to the mainland coast. Initially, convergence of the oceanic and continental plates of the western margins of Pangaea resulted in a deep offshore trench, steep coastal mountains, and little continental shelf. The North American coastline was extended by accretion of terrain carried eastward by the coastal subduction zone and plate convergence. The terrace forming the Alexander Archipelago of Alaska apparently separated from Australia 375×10^6 y.b.p. (Finn 1986). Approximately 50×10^6 y.b.p., the tectonic pattern changed in North America from a primarily convergent pattern, dominant in South America, to one of shear boundaries with northward transportation of accreted insular terrains. The general result was that the shelf remained narrow and the oceanic trench deep in Peru and Chile, while in the north the oceanic trench was filled with sediments eroded from the coastline.

Stages of Regionality

We now speculate on possible stages in the formation of faunal regionality of the Eastern Pacific Domain subsequent to the fragmentation of Pangaea. We utilize Dietz and Holden (1970) and the paleogeographical maps published by Smith and Briden (1977) to trace significant stages in the fragmentation process. Because the early fossil record of bivalves is too fragmentary to support our speculations, we draw from records of other groups.

The shelf fauna of Pangaea did not arise spontaneously on a *tabula rasa*, but from pre-existing fauna carried by the four continents that aggregated to form Pangaea (Ziegler et al. 1977). Already during the Ordovician ($\approx 500 \times 10^6$ y.b.p.) the Pangaean shelf fauna showed signs of regionality of conodonts (Bergstrom 1973; Sweet and Bergstrom 1974), graptolites (Skevington 1973) and trilobites (Whittington 1973). During the Silurian ($\approx 460 \times 10^6$ y.b.p.), European and Asiatic faunal regions were distinguishable (Kaljo and Klaamann 1973), indicating the possibility of latitudinal thermal gradients of the ocean (Cramer 1971). The Devonian ($\approx 400 \times 10^6$ y.b.p.) was a time of increasing provincialism, particularly of brachiopods, already markedly endemic and regional (Boucot et al. 1969). The period terminated with the extinction of many taxa (Boucot 1975), particularly of the tropical and subtropical zone molluscan fauna; however, this event left the cooler regions relatively untouched. By the Carboniferous ($\approx 350 \times 10^6$ y.b.p.), there existed strong regionality in corals (Hill 1973) and Foraminifera (Ross 1973), but significant cosmopolitanism in the general fauna persisted and those sections of the western continental shelf which would contribute to the formation of the Pacific coast of North America demonstrated obvious Tethyan affinity (Ross and Ross 1981). During the Permian ($\approx 270 \times 10^6$ y.b.p.), regionality increased, particularly in brachiopods (Waterhouse and Bonham-Carter 1975), while the latitudinal distribution of several other marine groups show evidence of increasing thermal heterogeneity of the global ocean (Stehli 1964).

The above superficial summary furnishes sufficient evidence to support the view that the fauna of Pangaea was complex and probably fluctuated between periods of faunal differentiation and homogeneity. By the early Triassic ($\approx 200 \times 10^6$ y.b.p.) Pangaea was an approximately circular supercontinent with lateral invaginations of the Protoarctic and Prototethys seas, surrounded by the global ocean (Panthalasia) (Fig. 7a). At this time, there probably existed a small but significant latitudinal thermal gradient in the ocean, together with a system of prevailing oceanic currents which could have influenced regionality of the neritic zone. It has been speculated that eight oceanographic regions with distinct faunas, equivalent to provinces, may have existed (Schopf 1979). However, the Permian/Triassic transition was a time of major extinctions and oceanic regression resulting in the impoverishment of the shelf fauna. This fact, and the evidence of the distribution of several shallow water marine groups, suggests eight provinces circling the continent is too high an estimate, and that at most four biogeographic zones equivalent to the contemporary province existed. The western half of Pangaea, regions that would form the west coast of North and South America, probably supported three poorly differentiated faunal regions.

Pangaea began to fragment during the Late Triassic ($\approx 200 \times 10^6$ y.b.p.) into northern (Laurasia) and southern (Gondwana) continents. This separation resulted in the Tethys Sea forming a complete circumequatorial ocean with a remarkably uniform biota, usually considered a single biogeographic region. The unobstructed Tethys Sea and the prevailing east to west current through the early Protocaribbean zone (Gordon 1974) are the dominant factors in the formation of the faunal components of the eastern Pacific tropical shelf (Croizat et al. 1974) and significantly influenced the entire Pacific and Indo-Pacific regions. The Tethys Sea continued to be the principal global marine feature for more than 100 million years. It attained its maximum development during the Cretaceous ($\approx 120 \times 10^6$ y.b.p.) when it comprised an extensive warmwater region with the 18°C isotherm extending to 60°N (Bandy 1964) and to a corresponding southern latitude (Fig. 7b).

By the Cenozoic ($\approx 60 \times 10^6$ y.b.p.), the geographical situation was almost contemporary (Fig. 7c), though the Caribbean Seaway remained open. Colonization of the Pacific sector of the Central American region continued and carried northwards, displacing the indigenous fauna. Closure of the isthmus of Panama during the Middle Pliocene ($\approx 3.5 \times 10^6$ y.b.p. or later) sundered the amphiamerican fauna into Pacific and Atlantic segments (Woodring 1966) and led to the contemporary situation (Fig 7d).

Patterns of Distribution

The transportation of continents due to plate tectonic movement rafted entire biomes to new positions, but superimposed on this simple spatial translation are several other factors directly contributing to regionality, the most important being climate. Early attempts at a biogeographical synthesis were largely climatological and based on latitudinal thermal zones (Zenkevich 1949a,b). This approach does in fact conform to reality when adjusted for prevailing ocean currents (Fig. 8). However, the boreal and antiboreal regions are faunally distinct and the early concepts of bipolarity summarized and developed by Farquhar (1908), Derjugin (1927) and Berg (1933) do not stand.

Similar environments contain similar communities, but the component organisms change. A clear example is the equatorial belt of coral reefs which occupy a substantially uniform physical environment, yet it is clearly distinguishable into distinct units. Similarly, the bivalves occupy ecological niches defined by environment acting on intrinsic physiological adaptability. However, organisms in general have significantly broader tolerances than that indicated by distribution, so other factors must be effective moderators or initiators of distribution.

Biogeography and evolution have been closely linked from their earliest inception (Darwin 1859; Wallace 1876). Trophic and competitive interactions undoubtedly play significant roles (Paine 1966); however, the availability of a suitable niche dictates whether a particular species

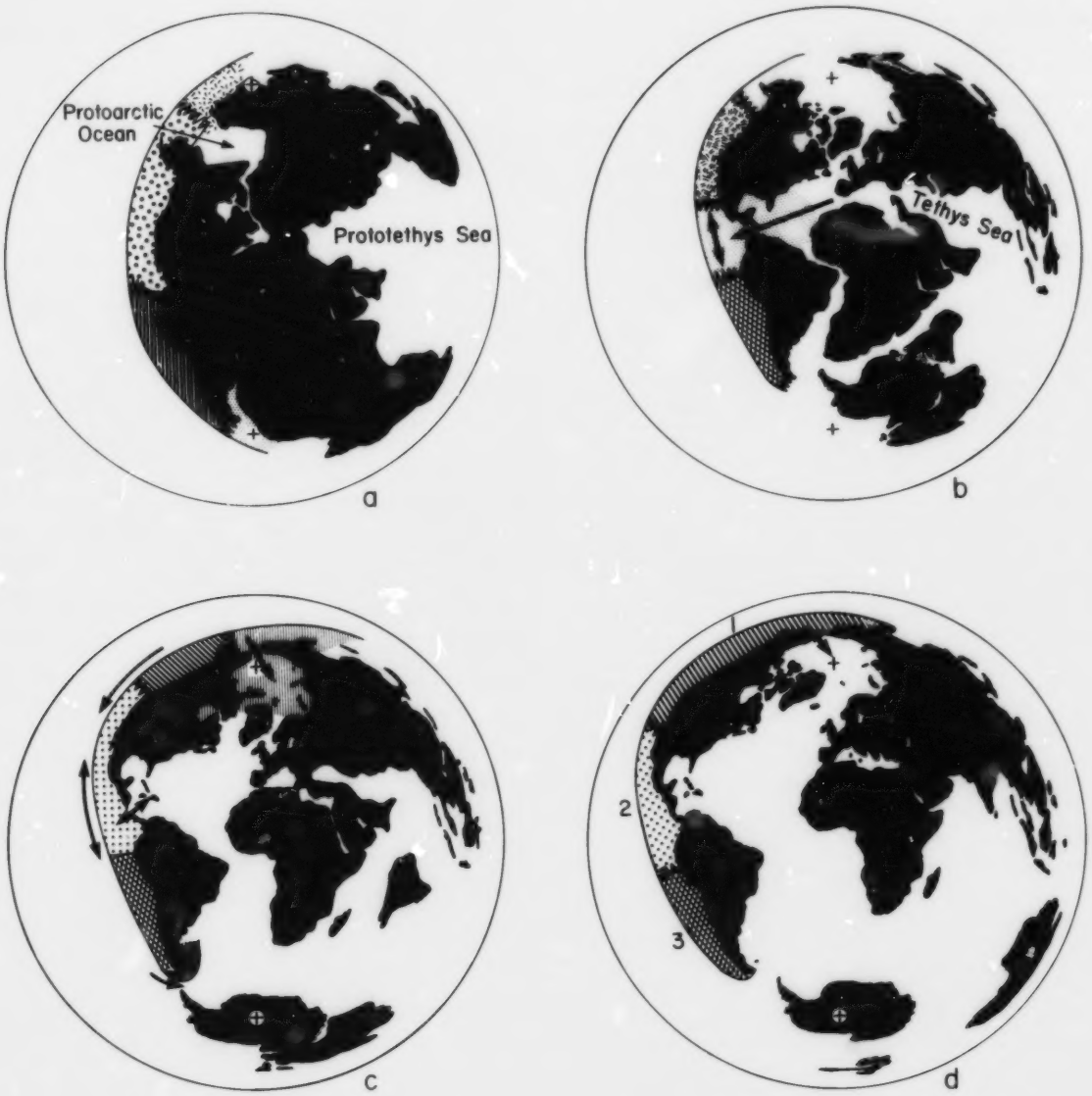

FIG. 7. Paleocontinental maps and postulated zoogeography of the neritic zones of the eastern Pacific Ocean. a) Early Triassic Pangaea (220 × 10^6 y.b.p.); b) Early Cretaceous (120 × 10^6 y.b.p.); c) Cenozoic (60 × 10^6 y.b.p.); d) present day. Lambert equal area projection (Modified from Smith and Briden 1977).

is present. All organisms exert expansionist pressure on distributional boundaries and usually outrider individuals occupy marginal habitat. Species, especially those with pelagic larvae, in favourable years will settle outside their established range (Shuto 1974; Scheltema 1977; Scheltema and Williams 1983). Examples are sporadic individuals of the bivalve *Pseudochama exogyra* (Conrad 1837) in British Columbia from established populations in central Oregon, and *Pinctada mazatlanica* (Hanley, 1856), a Panamic species abundant in Mexico but occasionally found in numbers off southern California. Though a planktotrophic larval stage favours wide dispersal, it does not appear to be selected primarily for this potential (Strathmann 1985). The transitory planktonic existence does not directly influence the evolutionary pattern, though pelagic organisms in general show gradual phyletic evolution (Malmgren and Kenneth 1981; Johnson 1982) while benthic organisms frequently undergo punctuated evolution (Hallam 1978). These differences may be overstated and may be the result of different depositional regimes of the deep and shallow environment and its influence on the fossil record (McKinney 1985).

Latitudinal Effects

The complex interplay of physical and biological factors dictate the quantitative (how many taxa, or faunal diversity) and the qualitative (which type of taxa) aspects

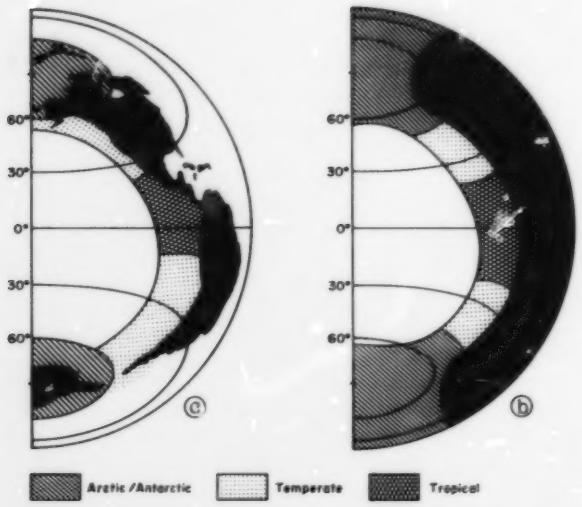

FIG. 8. Eastern Pacific Ocean marine climate zones. a) actual situation; b) generalized concept based on a uniform continental mass (Modified from Zenkevich 1949a).

of regionality. These are usually expressed as gradients in a latitudinal section. The most obvious example is the poleward decrease in diversity of neritic organisms, including the bivalves (Stehli et al. 1967) (Fig. 9). The low latitude diversity is apparent in the bivalve data for intertidal and subtidal 100 m zones. Though this pattern is universal (Kuronuma 1942) and extends back at least to the Permian (Stehli et al. 1969), no objective basis exists for considering the low latitudes to be more favourable than other regions for the proliferation and support of taxa. Conflicting hypotheses as to its cause have been advanced (reviewed by Pianka 1966). It has been speculated that low latitude diversity is the legacy of the circumequatorial Tethys Sea fauna that continue to occupy a region little subjected to the climatic change and other perturbations characteristic of the higher latitudes. It may be that stable environments permit development of specialization, thereby opening more niches and ultimately leading to increased diversity (Wallace 1878; Fisher 1960). However, the region of greatest stability, the deep ocean, does not support a very diverse fauna

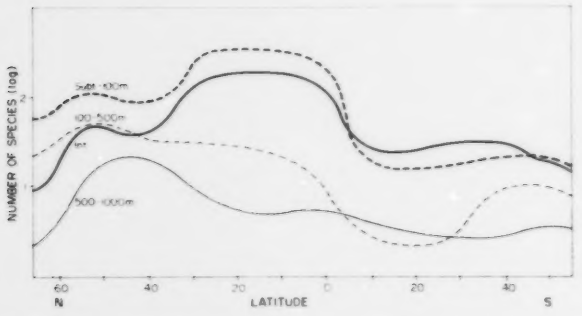

FIG. 9. Total number of living marine Bivalvia of the eastern Pacific Ocean by depth as a function of latitude. Int. = intertidal, Subt. = Subtidal.

in terms of either variety or number, and it is generally conceded that evolutionary change of deep-water fauna is substantially lower than that of comparable shallow water fauna (Levington 1973, 1974), and that maximum deep-water diversity occurs along the continental shelf and is associated with areas of deposition (Dickinson and Carey 1978). It may be speculated there are less, or fewer, unoccupied niches, at the higher latitudes. This concept hinges on the assumption that there is a maximum diversity number, after which exclusion occurs. However, this view is not supported by analysis of the effect of introduced species into established communities as in the majority of cases examined, no disruption was detected (Simberloff 1969). Our bivalve data for the 100–500 m and 500–1000 m zones reveal predominant species diversity in the northern Pacific that may reflect degree of collecting coverage.

Whereas there exist fundamental differences in energy flows through warm and cool ecosystems (Petersen and Curtis 1980), we do not share the general view that selection in the temperate and cold marine regions is primarily controlled by the physical environment, while biological interactions are the major determinants of evolution in the tropics (Dobzansky 1950; Williams 1964). Certainly, bivalves become more colourful and ornamented with decreasing latitude, but for bivalves at least there exists no objective evidence that greater population pressure exists in the tropics. In our opinion, the more stable food supply and increased niche availability will act to reduce competition, while the large mortalities resulting from unseasonable climate or unavailability of food, coupled with fewer niches, characteristic of high latitude neritic areas invariably lead to opportunistic life strategies and increased biological competition. Seasonality may also be a potent factor limiting diversity, but for most bivalves, seasonal shifts occur at a faster rate than the population can respond, so it is improbable that distribution can be simply limited by the unfavorable season. We agree that prolonged environmental stability may allow specialization and, ultimately, speciation, while a fluctuating environment results in a more generalized lifestyle able to exploit transitory food supplies (Preston 1962).

The hypothesis that predation pressure is greater in warm marine regions also requires re-examination. It is correct that, following prey diversity and development of specific antipredatory behaviours and structures, predators become more diverse and specialized to exploit a single, or at most, a small suit of prey species (Vermeij 1978). However, in terms of biomass, predators are significantly more abundant in temperate and cold shallow water regions. Further, intensity of competition is invariably not correlated to predators, abiotic stress or other ecological factors, so it does not follow that competition is greater in stressful situations (Welden and Slauson 1986).

If low latitude diversity is the direct result of an older, relatively undisturbed fauna which has had more time to diversify (Hecht and Agan 1972), it should be detectable in the relative paleontological age of the fauna. Tropical species should be significantly older than boreal and

antiboreal species. This is not supported by our data. Estimated relative paleontological age of living bivalves, made from maximum known age in West America (Recent = 1, Oligocene = 5), accumulated by latitude block means, demonstrates a clear trend of increasing age north to south (Fig. 10). There is an abrupt increase of age at approximately 35°N, probably connected with the southernmost extinction due to glaciation. There is also a region of decreasing age at 2°N to 9°S latitude, which may be associated with extinctions and speciation events connected with the closure of the Isthmus of Panama. The trend is uniform from the intertidal zone to depth, but is most obvious from the intertidal zone to 500 m depth: 55°N–28°N = 3.79 ± 0.55; 27°N–5°S = 4.40 ± 0.28; 6°S–50°S = 4.63 ± 0.43.

The suggestion that the intertidal zone bivalves are paleontologically older than the deep-water representatives is supported by our data (Table 3). However, the data are influenced by differential preservation. Deep-water faunas are poorly preserved, so most of the species are known only from the Recent. Virtually the entire known bivalve fauna of the depth below 2000 m is Recent, attributable to the absence of outcrops of deep-water origin. This may be an artifact due to fewer deep water facies represented in the geological record, or reflect the more recent colonization of the deep ocean after the abrupt decrease in temperature from an average 10°C during the Eocene (Savin et al. 1975) to its present value (~2°C) during the Middle Miocene (≈ 13 × 10^6 y.b.p.). It appears this change was not sufficiently gradual to allow evolutionary accommodation, as contemporary deep-water fauna is composed of relatively Recent migrants from the adjacent shelf and slope regions. It has been suggested that colonization of the deep ocean was initiated by the loss of neritic areas during major oceanic regressions and it was easier for the frigophilic polar elements to invade the cold, deep ocean than for the thermophilic shelf fauna of the lower latitudes (George 1977). Analysis by depth category of our data supports the older paleontological age of the shelf bivalve fauna. Our data reveal no statistically significant bathymetric cline in the relative age of bivalves of the shelf zone to the intertidal region, where the supposedly more eurotypic fauna is better able to withstand environmental change and perturbations (Jablonski 1980; Jablonski and Valentine 1981). In fact, our intertidal fauna is marginally younger. Tabulation of the extinction rates of various Paleozoic marine assemblages reveals that offshore communities have higher overall extinction rates, but that individual classes demonstrate highest overall extinction rates onshore (Sepkoski 1987). There is no evidence supporting the hypothesis that intertidal zone organisms display an enhanced potential for adaptation to environmental change. However, our data do agree with the contention that intertidal bivalves of the high and northern latitudes are significantly older than deeper shelf species. Jablonski et al. (1983) suggest that evolutionary changes start in the nearshore zone and then extend across the neritic area to the offshore setting. The question bears some examination, as by necessity, intertidal zone organisms must cope with wide and abrupt short-term environmental fluctuations; this is usually accomplished by suspension of activity and isolation from the inimical environment. Intertidal zone organisms are dependent on narrow environmental optima, particularly during certain key stages in the life-cycle. At such times, unexpectedly small deviations are sufficient to prevent gametogenesis or spawning, and may lead to mortality later in the season. Populations of the northern clam *Saxidomus giganteus* (Deshayes, 1853) and the cockle *Clinocardium nuttallii* (Conrad, 1837) do not spawn in cool years (F. Bernard, unpublished data), so reproductive success is temperature dependent for some bivalve species. Catastrophic and widespread mortalities of shore organisms have been recorded in all regions, but similar mortalities of subtidal zone dwellers are rarer. It is reasonable to conclude that relatively short-term and small environmental changes are sufficient to disadvantage intertidal zone organisms, but similar subtidal events are precipitated only by major and sustained perturbations.

The latitudinal and bathymetric distributions of the relative paleontological age of the bivalve fauna of the eastern Pacific Ocean are complex and require more detailed examination. Our data reveal only a slight age differential between the intertidal and shallow shelf (i.e. subtidal zone to 100 m) bivalves, except for the latitudes above 50°N where the difference increases but may be influenced by paucity of species (Fig. 11). A very significant latitudinal component is evident when comparing

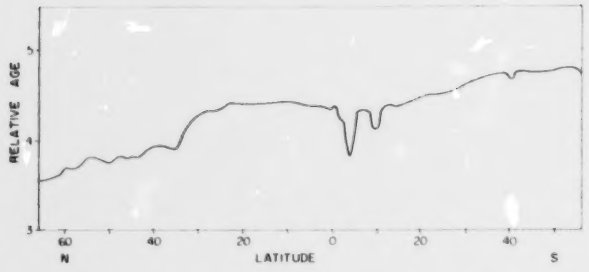

FIG. 10. Mean paleontological age (See Table 3: Recent = 1, Oligocene = 5) of living Bivalvia of the eastern Pacific Ocean from the intertidal zone to 500 m depth.

TABLE 3. Relative Paleontological age of the living marine Bivalvia of the eastern Pacific Ocean by depth category.

Depth (m)	Relative age[2]	SD
Intertidal	4.15	0.68
Subtidal - 100	4.58	0.95
100 - 500	4.30	0.60
500 - 1000	4.58	0.62
1000 - 2000	4.84	0.49
2000 - 3000	1.05	0.02
3000 - 4000	1.01	0.05

[a]Estimated: Recent = 1, Pleistocene = 2, Pliocene = 3, Miocene = 4, Oligocene = 5.

the intertidal zone to the deeper fauna. The high latitude subtidal fauna is older both in the Arctic and Antarctic regions, whereas differences are small in the middle and low latitudes. However, there exists a pronounced reversal of this trend between 5°S to 30°S, where the bivalve fauna on the continental slope at 500–1000 m is significantly older than the mean age of the intertidal zone fauna. The anomaly is carried into the shallow shelf zone (subtidal zone to 100 m), so the observation is probably factual and suggests that the intertidal zone bivalve fauna of the Peru–Chile region is of relatively Recent composition, possibly derived from the adjacent deeper shelf zone or a consequence of extinctions attributable to changes of sea level associated with the glacial cycle.

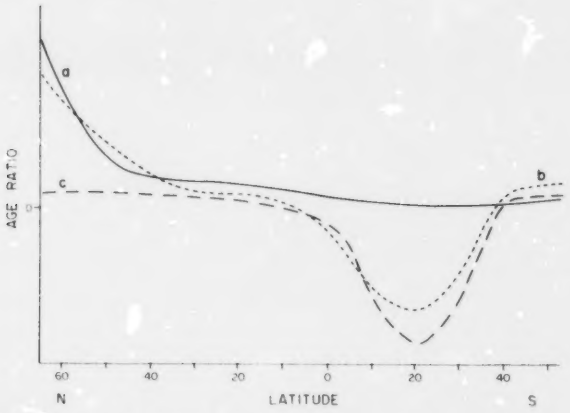

FIG. 11. Relative differences in the mean paleontological age of the marine Bivalvia of the eastern Pacific Ocean as a function of latitude and depth. a) intertidal zone compared to subtidal zone — 100 m; b) intertidal zone compared to 500–1000 m; c) subtidal zone — 100 m compared to 500–1000 m.

Distribution and Environment

There may also exist a relationship between palaeontological age and geographic distribution, summarized by the dictum: the older the taxon, the wider the distribution (Bretsky 1973). However, our data did not indicate any significant relationship among the ages of living bivalve families aggregated into 30° latitude blocks, nor a correlation of these with the estimated age of the ocean floor (Fig. 12). Fitted regression lines for the living families, genera, and species of the bivalves of the eastern Pacific Ocean do demonstrate an increasing mean latitudinal range from species to genus to family (Fig. 13). Part of this trend may be simply explained as the result of progressively amalgamating groups into fewer cells.

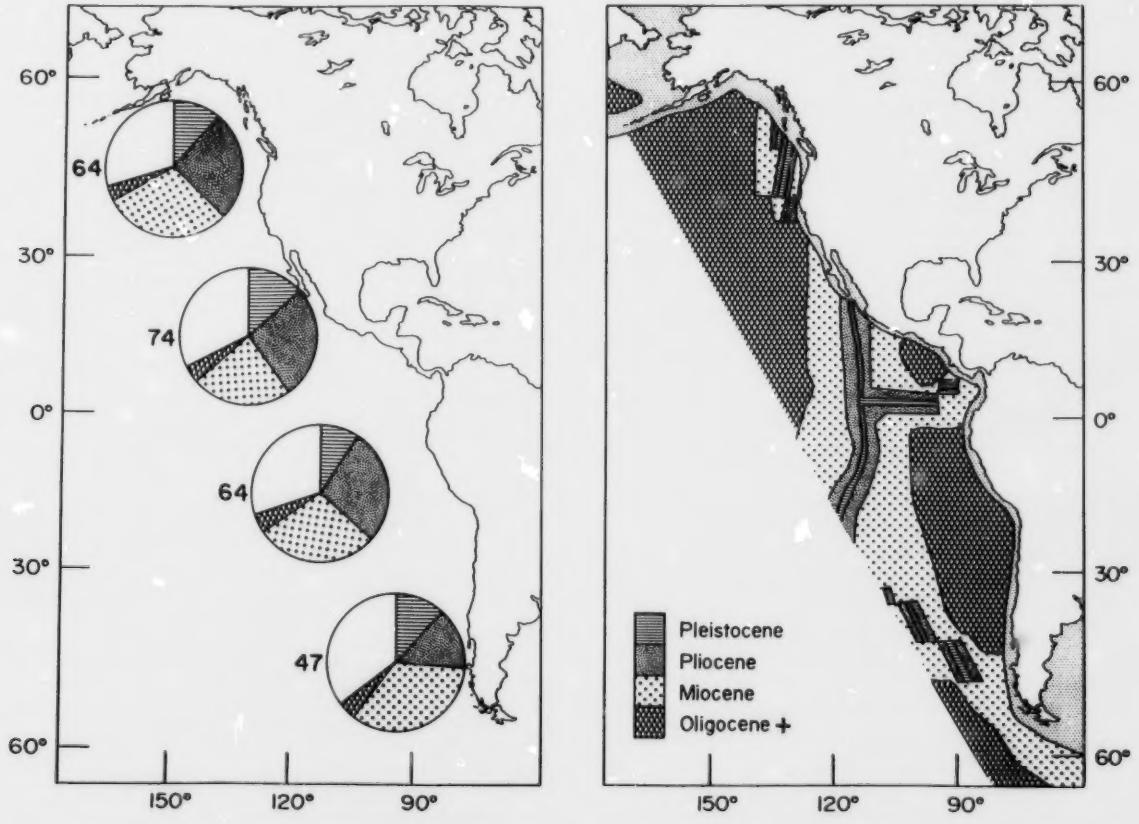

FIG. 12. Relative occurrence by geological age *(left)* of the families of living Bivalvia of the eastern Pacific Ocean compared to mean age of the sea-floor *(right)* (Modified from Pitman et al. 1974). Blank = Recent; Numbers indicate number of families in each 30 latitudinal block.

However the fitted lines do indicate increased distribution with geological age for genera and families. This pattern is not repeated at the species level where there is no significant effect of increasing age on latitudinal distribution.

While no comprehensive hypothesis linking environmental temperature to faunal diversity has been advanced (Rohde 1978), the major cause of latitudinal gradients in diversity may be related to thermal regimes (Dow 1973), being inversely correlated to seasonal temperature range (Sanders 1968; MacArthur 1975) (Fig. 14). Comparison of bivalve species occurrence with mean annual surface temperature reveals a strong positive correlation in the case of intertidal species (Fig. 14a), a better fit than that shown with any other environmental parameter. Similar comparison of the subtidal zone-to-100 m fauna to the mean annual temperature at 100 m demonstrate a less clear, but nevertheless positive, correlation (Fig. 14b), with the exception of the southern hemisphere where the Chilean fauna is little affected by temperature. Decreasing average temperature polewards has been a salient marine factor since at least the Middle Miocene ($\approx 13 \times 10^6$ y.b.p.) and has been a potent cause of regionality (Addicott 1970, 1977).

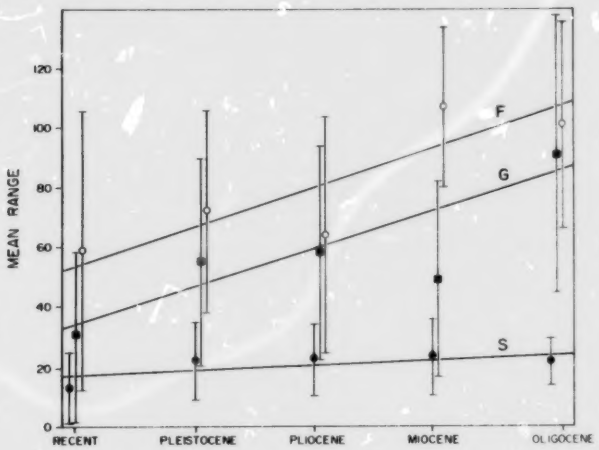

FIG. 13. Fitted regression lines of mean latitudinal range in degrees of latitude of the families (F), genera (G), and species (S) of living Bivalvia of the eastern Pacific Ocean.

Ocean Temperature

The fossil record reveals a long history of changing ocean temperature with associated faunal displacement and marked periodicity of extinctions (Raup and Sepkoski 1984). During the Middle Oligocene ($\approx 30 \times 10^6$ y.b.p.) sea temperature was at a minimum (Tipton et al. 1974) and the equatorial Pacific Ocean was substantially colder than at present (Douglas and Savin 1971). The fauna of the Gulf of Alaska extended far southwards and little provinciality was evident. In the Eocene ($\approx 20 \times 10^6$ y.b.p.), there occurred a warming phase discernible both on the eastern (Wolfe and Hopkins 1967; Axelrod and

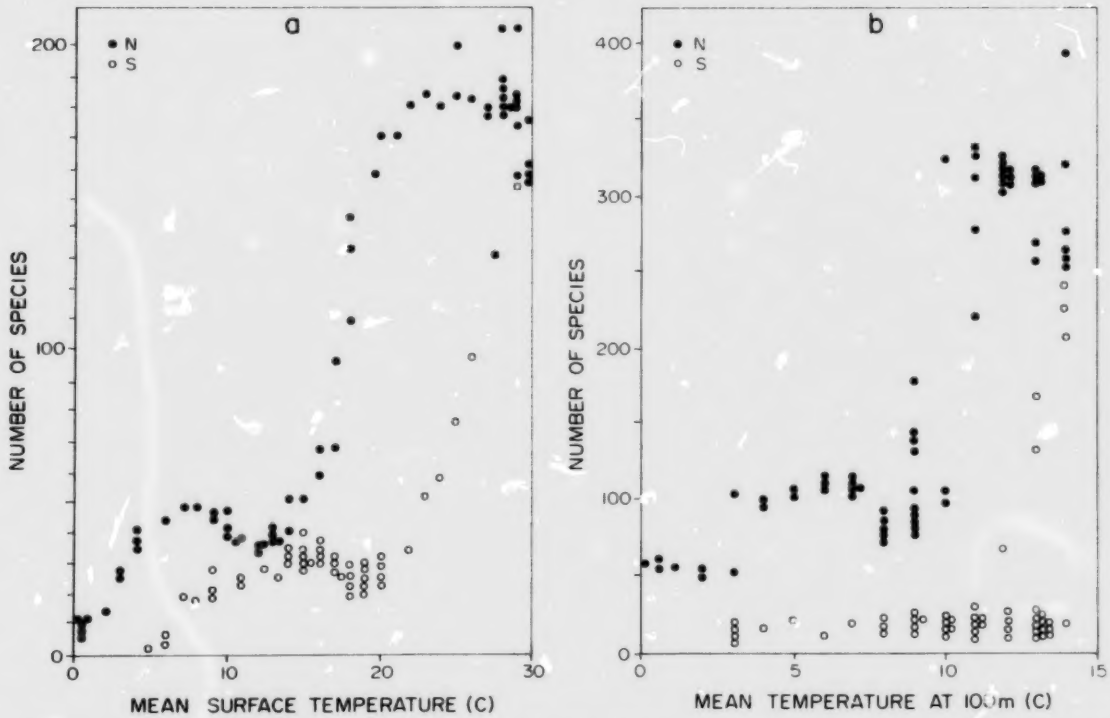

FIG. 14. Number of species of living bivalves in each hemisphere of the eastern Pacific Ocean in relation to mean annual temperature (°C). a) intertidal species and mean annual surface temperature; b) subtidal — 100 m species and mean annual temperature at 100 m (from Levitus 1982).

Bailey 1969) and western (Dall 1893; Pronina 1969) sides of the North Pacific Ocean. At this time, the shelf fauna of the northeastern Pacific Ocean was distinctly subtropical and penetrated north and west (Moore 1964; Allison 1978) to encompass Eastern Beringia, Northern Japan, Sakhalin, the South Kurile Islands, and eastern Kamchatka (Oyama et al. 1960; Takai et al. 1963; Krishtofovich 1964; Pronina 1969). This oceanic warming was global and modified faunal distribution patterns of South America (Devereux 1967; Margolis and Kennett 1970). It also permitted faunal exchange between the North Pacific and North Atlantic Oceans through the Arctic Basin. The warm trend continued through the Miocene (Itoigawa 1978) when tropical faunas extended to 50°N in the North Pacific (Addicott 1969), to be followed by cooling during the Late Miocene which exterminated many taxa. The minor warming phase of the Pliocene (4×10^6 y.b.p.) (Douglas and Savin 1971; Armentrout et al. 1978) resulted in latitudinal migration of the neritic fauna. By the late Pleistocene, four molluscan provinces were discernable in the northeast Pacific roughly corresponding to the contemporary situation (Addicott 1966). Fossil deposits show a rapidly changing sequence of warm or cold water species, representing the dynamic thermal regimes of the time (Kennedy et al. 1982).

Most paleoclimatic evidence suggests widespread global synchronism. Late glacial epochs appear to be contemporaneous in the North and South American Pacific and conform to events in the North Atlantic (Auer 1966). Correlation of the five Pleistocene glaciations and several Recent glacial advances in Alaska (Karlstrom 1966) are broadly in phase with the Milankovitch solar radiation curves. The position of the American continental mass relative to the equator doubtless affected general climate. The northwest migration of North and South America moved the effective latitude of the Gulf of Alaska northwards. This displacement was possibly initially counteracted during the Early Jurassic ($\approx 180 \times 10^6$ y.b.p.) by an apparent shift of the geographic poles. There exists evidence, based on paleomagnetic data and the premise that the hot-spots framework associated with volcanic features is nearly fixed or only slightly moving (Kerr 1987), while the lithosphere is moveable, of substantial displacement of the polar axis some 22° ± 10° to a position off northern Europe (Andrews 1985). This would in effect move the Pacific equator 22° northwards. A movement of that magnitude can only be interpreted as the result of shifting of the entire lithosphere, probably responding to a change in the principal axes of the moment of inertia of the mantle. The drift of the American continental mass due to plate tectonics combined with shifting of the polar axis at a rate comparable to continental drift (Sager and Bleil 1987) has profound biogeographical implications. During maximum polar migration, the Tropic of Cancer fell in the region of Cape Mendocino (40°N) and the temperature of the Gulf of Alaska waters could have increased 5–8°C. The continued shifting of the geographical pole could have reversed the trend approximately in the Middle Cretaceous (100×10^6 y.b.p.) and depressed the equator 11° southwards by the Late Cretaceous. At this time the Tropic of Cancer would be located off Nicaragua (11°N) and the Gulf of Alaska could have been cooled to 3–5°C below its present temperature. Some of the climatic implications of the shifting polar axis hypothesis correlate well with fossil facies of the North Pacific region, but much careful investigation of global paleoclimates and continental migrations are required to arrive at a synthesis of this interpretation.

Thermally mediated faunal migrations set the pattern of contemporary distribution and to some extent dictated the taxa currently present (Hutchins 1947). It is recognized that a significant portion of northeastern Pacific bivalves originated in the Asiatic sector (i.e. *Mya, Patinopecten, Panomya*, etc). The dominant colonizing movement throughout the Cenozoic has been eastwards, and during much of this time there existed a continuous coast joining Asia and America, while the Sea of Okhotsk and the Sea of Japan were occupied by land (Sergeev 1976). The pattern of northward penetration of the fauna during warm phases, followed by retirement southwards, was sufficient to transfer elements between the western and eastern sectors of the North Pacific Ocean; it is not necessary to invoke dominant current patterns.

Effects of Change in Sea Level

Prior to the fragmentation of Pangaea, and especially since the Quaternary Period, there have occurred numerous changes in sea level associated with the glacial cycle. During the maximum extent of glaciation, sea levels decreased as much as 160 m (Kurten 1972) while during interglacial periods, sea levels were 70 m above the present level (Fairbridge 1973). This eustatic cycle, coupled to isostatic changes due to crustal warping and adjustment of continental elevation, drastically altered the area of continental shelf, which at times was entirely exposed (Vail et al. 1977). Such oceanic regressions are significantly correlated to mass extinctions of the shelf benthic fauna, but it is not clear if this is the direct result of loss of habitat or is associated with alterations in the water column exchange. These changes in relative sea level were global, and shelf faunas of the glaciated latitudes were particularly vulnerable as the remnants of the continental shelf was ice covered or scoured. As glacial episodes were nearly contemporaneous in the northern and southern hemispheres (Flint 1957; Auer 1960), the shelf faunas of the higher latitudes were locally extirpated and displaced towards the equator (Newell 1962). As conditions ameliorated and ice retreated, the newly available territory was colonized by a process of zone-invasion (Setchell 1920) from the adjacent lower latitudes and the refugia that play an important role in the North Pacific region (Hopkins 1979). The southward retreat of North Pacific species is known to have preserved numerous taxa from extinction. In the northeastern Atlantic Ocean and Caribbean Sea, such migrations were not possible because of geography and in these regions climate-related extinctions were much more severe.

Living and Fossil Distributions

Climate induced displacement of the shelf fauna allows comparison of the distributions of living and Quaternary fossil faunas by noting the sums of the arithmetic means of latitudinal distribution and calculating a theoretical mid-point for the entire assemblage (Schenck and Keen 1940). It has been argued that mid-point of distribution has no biological significance, as ranges are not skewed (Newell 1948), but this interesting observation cannot be lightly dismissed, especially as it has offered a useful palaeoecological tool. The bathymetric and geographic ranges, as well as oldest North American occurrence, are summarized in the appendices for genera (Appendix 1) and families (Appendix 2). The presence or absence of a particular species should correlate closely with environmental parameters and be influenced by such localized phenomena as upwelling, so it may be expected that the accumulated means of distribution will be a sensitive indicator of faunal displacement. This is evident in contemporary faunas (Kennedy 1982), indicating partial and incomplete latitudinal adjustment. However, it is simplistic to interpret such faunal latitude deviation as a simple displacement of a province still undergoing adjustment to environmental perturbation. It is in fact the sum of all distributional ranges and is sensitive to the type of distributional pattern predominating and the proximity of points to areas of significant faunal change. Where distributions of constituent species are shifting regularly with latitude, the deviation will be small. On the other hand, where the distribution pattern is grouped, deviations may be large and change in a regular way. The counteracting contributions of species with changing ranges and those with grouped ranges, as well as proximity of faunal boundaries imposing the latter condition, are the overriding factors deciding the size and direction of latitudinal deviation. No direct correlation to temperature is demonstrable. Calculation of the mid-points of distribution for all bivalves occurring in one degree latitudinal blocks along the eastern Pacific shelf reveal a pattern of displacement from the latitude of collection that is consistent with this interpretation (Fig. 15, Appendices 3, 4). The size and direction of the deviation of the faunal latitudes calculated here reveal an extension of the regular patterns first shown by Schenck and Keen (1940) for the northeastern Pacific coast of America. In the intertidal zone there is a stepwise decreasing trend between 60°–39°N which may be interpreted as a large-scale shifting of individual species ranges with latitude, together with decreasing number of species with extensive ranges. In short, increasing diversity with decreasing range. Latitudinal deviations are at a minimum at 39°N; there then follows an extended region of gradual replacement by more southern species. The largest southward displacement occurs in the Mexican intertidal bivalves, mostly due to the northward extension of distributional end points in the Gulf of California.

Differences Between Intertidal and Subtidal Elements

There exist differences between the latitudinal deviation of intertidal and subtidal zone bivalves in three areas that are statistically significant (Appendices 3, 4). Between

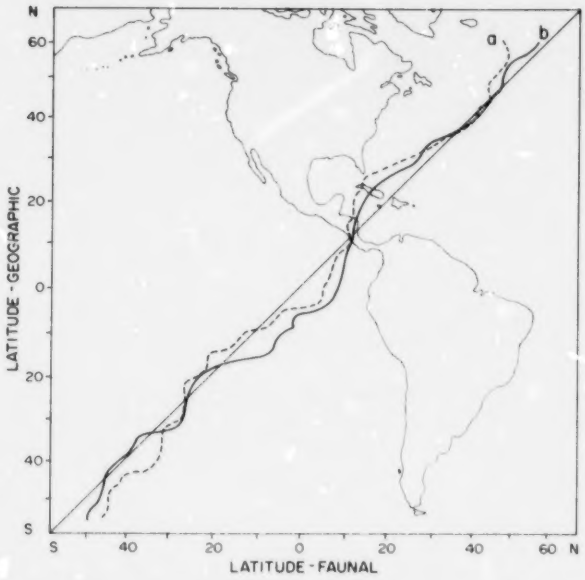

FIG. 15. Faunal latitudes calculated from mid-points of distribution of the living Bivalvia of the neritic zones of the eastern Pacific Ocean. a) intertidal; b) subtidal — 100 m.

60°–57°N ($p = 0.008$) the bivalve fauna is displaced further southward for intertidal species (Fig. 15). This may be an effect of the greater southward extension of the intertidal species and may be an indicator of depth specific provinciality which will be discussed later.

The area between 5°–15°S ($p < 0.001$) is one of strong deviation, particularly in the subtidal bivalves which are displaced polewards. This may be due to the northward penetration of frigophilic species in the intertidal zone. 5°S appears to be a major transition zone. To the south diversity decreases more rapidly in the subtidal than in the intertidal zone and more species are restricted to the intertidal than in deeper water. It is possible that at least a portion of these observations are artifacts due to collection coverage.

The area between 34°–43°S demonstrates marked differences ($p < 0.001$) between the intertidal and subtidal zone deviations. In the intertidal zone, the bivalves are shifted strongly toward the South Pole while in the subtidal zone they are shifted slightly towards the equator. This is the sole region in the eastern Pacific where latitudinal deviations of the two zones are opposite. This pattern may be attributable to the cold surface waters and low atmospheric temperatures allowing northward penetration of Antiboreal intertidal fauna. The subtidal bivalves are not significantly displaced and may reflect the older, more stable subtidal fauna known from few species of limited geographic range.

Species–Area Relationship

The effect of the species–area relationship on latitudinal diversity must also be examined. It is evident that the larger of two areas generally is richer in species (Gleason 1922; Flessa and Sepkoski 1978; and see review

by McGuinness 1984) and this relationship may be expressed mathematically (Connor and McCoy 1979). Obviously, faunal diversity is a function of the partitioning of available resources, so niche subdivision is initially exponential but reaches an asymptote as equilibrium is approached. This is the case for bivalves (Newell 1971). However, no direct relationship between neritic area and bivalve diversity has been demonstrated (Newell and Boyd 1978). A plot of total number of eastern Pacific living bivalve species per census block, as a function of area of the continental shelf, demonstrates no significant correlation (Fig. 16). There is evidence of a clustering of the small number of southern species with which may be due to insufficient collecting. The other cluster of extremely low diversity, as compared to available area, is in the Bering Sea. According to Schopf et al. (1978), tropical latitudes comprise more than twice the area of boreal regions. This contention is difficult to accept, as by far the most extensive shelf areas are boreal (Sea of Okhotsk, Bering Sea, Chukchi, Siberian Sea, etc). Adjusting for width of the continental shelf, ignoring local slope and topography and examining the shallow subtidal zone bivalves only, we obtained no significant correlation for the bivalves of the continental shelf area (Fig. 17). Similarly, an area factor may be injected by considering for the intertidal zone latitudinal differences on tidal amplitude (Fig. 18), but again, we were unable to detect any significant effect.

Bathymetric Distribution

It remains to examine the effect of bathymetric position on latitudinal distribution and diversity. It has been suggested that intertidal zone organisms are more restricted bathymetrically and geographically than those occupying subtidal areas (Menzies et al. 1973). Other analyses conclude that there exists significantly greater latitudinal range for the intertidal zone organisms (Jackson 1974; Jablonski and Valentine 1981). There is no evidence in our data that the intertidal zone bivalves have a distribution significantly different from those of deeper waters. However, there is a small latitudinal effect evident as those species from higher latitudes do show more extensive distribution patterns, irrespective of bathymetric range. The reason may be that dispersion is easier for frigophilic species which may invade lower latitudes by submergence to cooler depths, as first noted by Forbes (1844). The weaker thermal gradient between shallow and deeper water in polar regions may permit the emergence of deep-water taxa to shallow or intertidal areas. Should this hypothesis be correct, the ratio of exclusively intertidal zone bivalves to those extending to subtidal areas should be minimal in the high latitudes. This is the situation in the northern hemisphere and a strong linear relationship is evident from north to south (Fig. 19). It does not apply in the southern hemisphere, where the slope is almost zero between 0°–50°S and variance is greater than in the northern hemisphere. Factors other than temperature seem to operate, as Boreal subtidal zone bivalves frequently penetrate to depth while those from an equivalent Antiboreal area show a significant limitation to the intertidal zone.

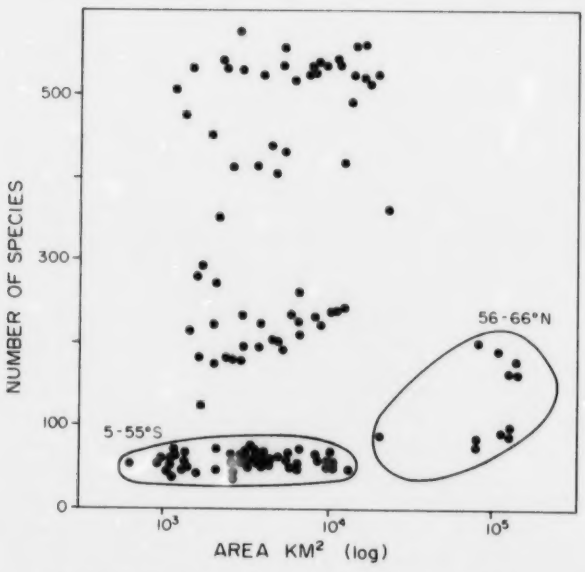

FIG. 16. Total number of living marine Bivalvia of the eastern Pacific Ocean, assuming continuous distribution, as a function of area of the continental shelf. (Calculated from MEDS, Department of Fisheries and Oceans, Canada.)

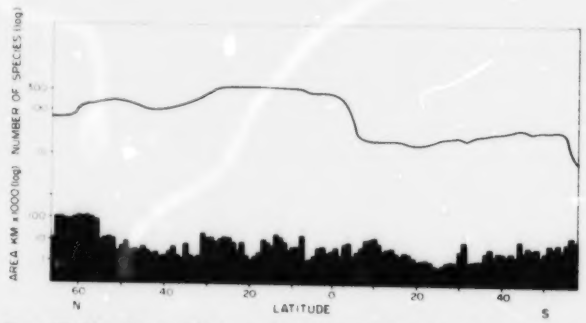

FIG. 17. Numbers of living subtidal zone Bivalvia of the eastern Pacific Ocean compared with latitudinal area of continental shelf to 200 m. (Width calculated from digitised bathymetric map, Maritime Environmental Data Service, Department of Fisheries and Oceans, Canada.)

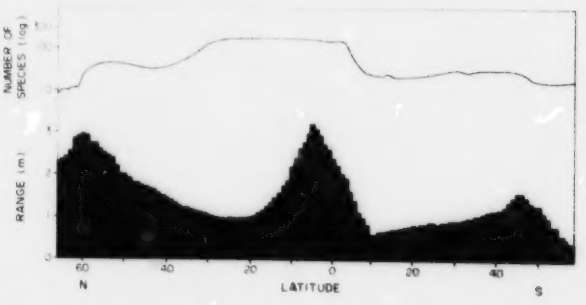

FIG. 18. Numbers of living intertidal zone Bivalvia of the eastern Pacific Ocean compared with mean tidal range (tidal means from Schwiderski 1979).

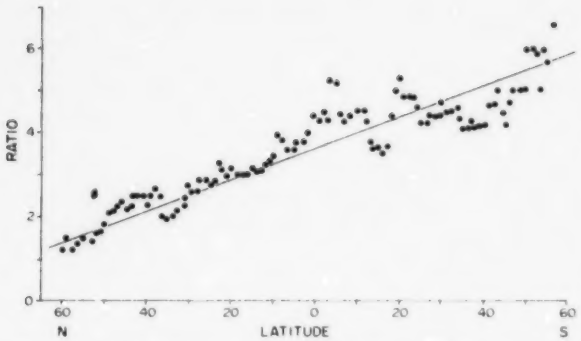

FIG. 19. Ratio of exclusively intertidal zone to subtidal zone marine Bivalvia of the eastern Pacific Ocean as a function of latitude.

To test if submergence is a significant factor influenced by latitude, six bivalve faunules were selected to represent cold, temperate, and tropical latitudes. To accumulate sufficient records for analysis and reduce purely local effects, occurrences one degree north and south of each transect were included. A non-parametric sign-test was used to test the hypothesis that change in latitude does not influence depth range. Results showed that the bathymetric range of 20 bivalve species occurring both at Kuskokwin Bay, Alaska (60°N), and Vancouver Island, British Columbia (49°N), is significantly greater ($p < 0.05$) in British Columbia both in terms of maximum and minimal depth (Appendix 5). This clearly supports the submergence hypothesis. In contrast, 42 bivalves occurring both at Dixon Entrance, British Columbia (54°N), and at Cape Mendocino, California (40°N), showed no significant overall differences in penetration to depth, but there did exist a small increase in total bathymetric range (Appendix 6). Sixty species occurring both at Manzanillo, Mexico (12°N), and Bahia Solango, Colombia (6°N), showed no significant differences in bathymetric distribution (Appendix 7). In all situations, the upper limit of bathymetric distribution is more abrupt than the lower, where outriders are frequent, especially where some protection from predation is afforded.

The apparent decrease of diversity (Vinogradova 1962) and biomass in the deep ocean region (Rowe et al. 1974) has been attributed to the paucity of food (Rowe 1971; Sokolova 1972). The decrease appears to be a function of depth rather than substrate, as the benthopelagic plankton shows similar trends (Wishner 1980). It may also be due to our lack of knowledge of the deep fauna, as those areas subjected to intense study reveal a substantial degree of diversity (Hessler and Sanders 1967) and these organisms are as genetically variable as their shallow-water counterparts (Gooch and Schopf 1972).

The stable environmental conditions of the deep ocean and widespread distribution of some abundant abyssal species led to the belief that abyssal fauna is cosmopolitan (Knudsen 1970; Sylvester-Bradley 1971). However, there is significant increase of endemicity with depth (Zenkevich 1963), and the majority of bivalves are not widely distributed but are limited to a single oceanic basin (Clarke 1962; Sanders and Hessler 1969). Vinogradova (1959, 1962) recognized one province below 4000 m in the eastern Pacific Ocean and this was followed by Menzies et al. (1973), who adjusted boundaries to more closely conform to basin topography and the overlying water masses. Surface productivity appears to be a potent factor determining benthic biomass (Rowe et al. 1974), which coincides with depository regimes (Muromtsev 1963; Geitzenauer et al. 1979), though persistent deep-ocean currents also play a role (Rowe 1983).

Bivalve Zoogeography of the Eastern Pacific Ocean

We have speculated briefly on the probable origin of the Eastern Pacific Domain; it is composed of rafted faunules from two continents (Laurasia and Gondwana) and one migrant fauna of Tethyan origin. We have discussed the role of climate and physiology in the formation of contemporary distributional patterns and their modification by latitude and depth. We now turn to the segregation of recorded distribution of the bivalve fauna of the eastern Pacific Ocean into zoogeographic units. Though mathematics may be used, the basic premises remain subjective and there continues to be considerable variance in the number and placement of boundaries according to the literature (Table 4).

A factor that must be addressed prior to a chorological analysis is the significance of discontinuous distributions. A preliminary analysis showed that assumption of a species' continuous distribution between end-points had no significant effect on conclusions. Discontinuities are present throughout the region and may be high where the total population is low and poorly explored. This is the explanation for the high proportion of range end-points at 33°S and at Cabo de Hornos (56°S) (Fig. 20). Adjusting for these artifacts reveals only two significant nodes, one at Point Conception, California (34°N), and the other at Punta Aguja, Peru (6°S).

Ocean Currents

We have noted the possible role of ocean currents in transportation of teleplanktonic bivalve larvae and speculated that dominant ocean currents may be potent factors controlling faunal distribution (Reid et al. 1978). Three major ocean currents recognized as affecting distribution of organisms (Bartsch 1921) move eastwards across the Pacific and impinge on the American continent (Fig. 21). These broad streams of water have velocities varying between a few centimetres a second to 90 cm/s (McCoy and Sancetta 1985) in parts of the Kuroshio supplying the Subarctic Current. In the North Pacific Ocean, the broad Subarctic Current separates offshore into the northern Alaska Current and the southward flowing California Current (Reid et al. 1958; Tabata 1975). The California Current leaves the coast off central Baja California and joins the westward flowing North Equatorial Current. The tropical Eastern Pacific is modified by the Equatorial Countercurrent which will be discussed in connection with the fauna of the Oceanic Islands. The South Pacific Current separates into the northern Peru Current and the southward Cape Horn

TABLE 4. Provincial boundaries based on the distribution of molluscs drawn from selected publications.

Location	This paper	[a] Hayden and Dolan 1976	[b] Hayden and Dolan 1976	Valentine 1966	Hall 1964	Olsson 1961	Knox 1960	Mann 1954	Balech 1954	Newell 1948	Schenck and Keen 1936	Dall 1921	Bartsch 1912	Dall 1899	Fischer 1887	Woodward 1856
68°N Seward Peninsula		X	X	X										X	X	
60°N Nunivak Island	X			X												
59°N Prince William Sound				X												
58°N Bristol Bay				X		X										
54°N Dixon Entrance		X	X	X									X			
48°N Puget Sound			X	X	X					X	X				X	X
40°N Cape Mendocino			X										X			
37°N Monterey Bay		X		X	X											
34°N Point Conception	X	X		X	X	X				X		X	X	X		
3[illegible]°N Cabo Lobos						X										
28°N Isla Cedros				X	X					X						
23°N Cabo San Lucas		X	X	X	X	X			X	X	X		X		X	X
25°N Bahia Magdalena	X															
9°N Bahia de Coronado		X														
2°S Guayaquil							X									
4°S Cabo Blanco	X	X	X			X			X							
5°S Paita																X
6°S Punta Aguja						X										
12°S Callao		X	X					X								X
27°S Caldera									X							
30°S Coquimbo							X									
33°S Valparaiso		X	X						X							X
36°S Talcahuana						X										
37°S Conception																X
42°S Puerto Mott						X	X	X								
47°S Golfo de Penas			X						X							
53°S Isla Desolacion			X													
56°S Cabo de Hornes							X									

Current. The Antarctic Circumpolar Current flows eastwards, but has little faunal impact. Because of the distances involved, the three great transpacific currents are not potent transporters of Indo-Pacific faunal elements to the American sector, but are the dominant mediators of productivity of the euphotic zone and so play a significant role in determining abundance of organisms. However, the along-shore limbs of these currents are major determinators of faunal migration and thermal regimes, and it is the locations where these currents leave or impinge on the shore that the major faunal breaks occur. This may be seen at the temperate-tropical transition off southern Baja California where the California Current sweeps westwards, and most especially, with the Peru Current carrying cool and temperate fauna far into the low latitudes. In the northeastern Pacific Ocean, the Alaska Current warms the coastal region from Vancouver Island around the Gulf of Alaska and into the Bering Sea, to a large degree compensating for expected latitudinal temperature change and resulting in a remarkably uniform fauna.

Provincial Units

We now proceed to allocate the total coastal bivalve fauna of 1229 species to provincial units using both principal coordinates analysis and clustering techniques. Although the results of clustering analysis are not described here in detail, in general, they agreed with principal coordinates analysis. For the latter, the total incidence data matrix, combining all depths but not assuming continuous ranges between end-points, provided an objective view of the general pattern of distribution (Fig. 22). The plotted points are one degree blocks of latitude. Their proximity to other latitudinal blocks is based on their similarity. As this type of figure is a projection of latitude ordination from a higher dimension onto two dimensions, there is some distortion, but it reflects both the polar impoverishment of the fauna and the species density gradient. The horizontal axis is a function of the number of species present, while the vertical axis reflects diversity. The grouping generated by this analysis follows

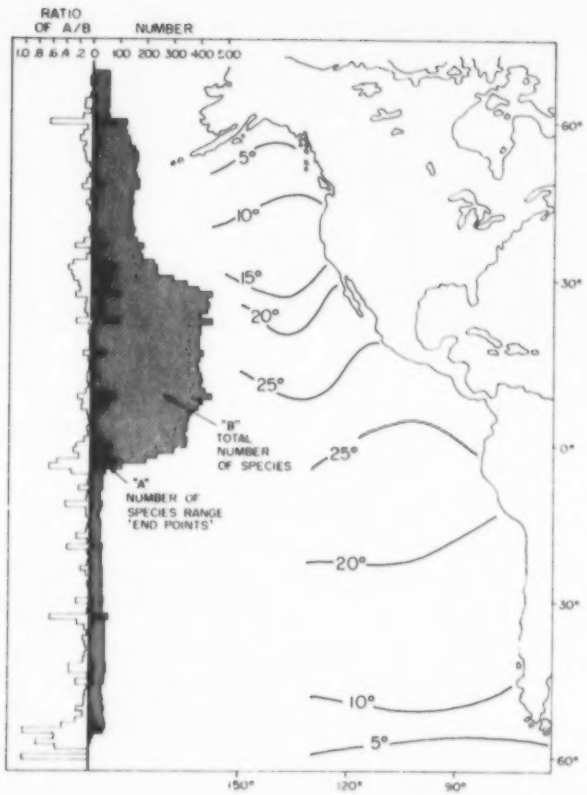

FIG. 20. The ratios of the number of bivalve species whose ranges end at each latitude to the total number of bivalve species present at that latitude. Species ranges were assumed continuous between end-points. Temperatures from Levitus (1982).

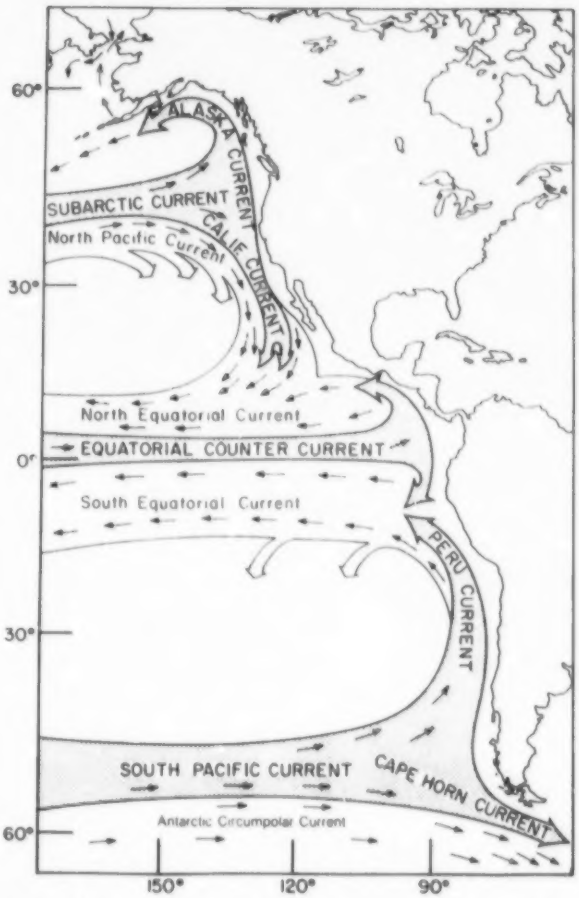

FIG. 21. Major currents of the eastern Pacific Ocean (modified from Tabata 1975, 1976).

the more conservative classical arrangement of provinces. Southern latitudes are generally on the left side of the plot and northern latitudes on the right. Interestingly, data extremes on the horizontal axis are 60°N and 5°S. This probably reflects the more complex structure of the bivalve fauna north of 5°S. Note that the Gulf of California appears in the lower left corner. This indicates that the species mix in the Gulf is more closely aligned with the Panamic fauna and potentially an integral part of it. However, although it appears with the South American latitudes, the Gulf of California is segregated. The vertical axis seems generally to correspond with the numbers of species at latitude. The exception is Point Conception, California (34°N). With relatively few species, the fairly diverse South American fauna forms a compact vertical cluster. The arrangement is a clockwise sweep, commencing and terminating with boreal and antiboreal faunas which are brought into juxtaposition as the result of faunal impoverishment.

The members of the most northerly group consist of all latitudes north of 47°N. No separation of Arctic latitudes (north of 60°N) is evident. A minor break occurs at Cape Flattery, Washington (48°N), that may be considered a subprovincial marker. It delineates the Washington subprovince and is probably at least partially correlated with the dichotomy of the Subarctic Current into northern and southern limbs. The next group includes all latitudes from 47°N south to the region of Point Conception (34°N), which marks the southern boundary of the Oregonian Province. The third group extends down to the Los Inocentes, Baja California, area (23°N). The final major break is near Paita, Peru (5°S). This analysis failed to demonstrate evidence of discontinuities on the southern South American coast except for a minor break at Valparaiso (32°S) due to incursion of Magellanic species.

Having arrived at an allocation of the general bivalve fauna into latitudinal clusters, it is necessary to determine whether the boundaries have any bathymetric component. It may be argued that bathymetry is equivalent to terrestrial distributions factored by elevation, and it is unlikely that a single province can embrace a significant depth range. According to Jablonski and Valentine (1981), provincial boundaries do in fact carry the shelf fauna to at least 100 m depth. This agrees with the observation

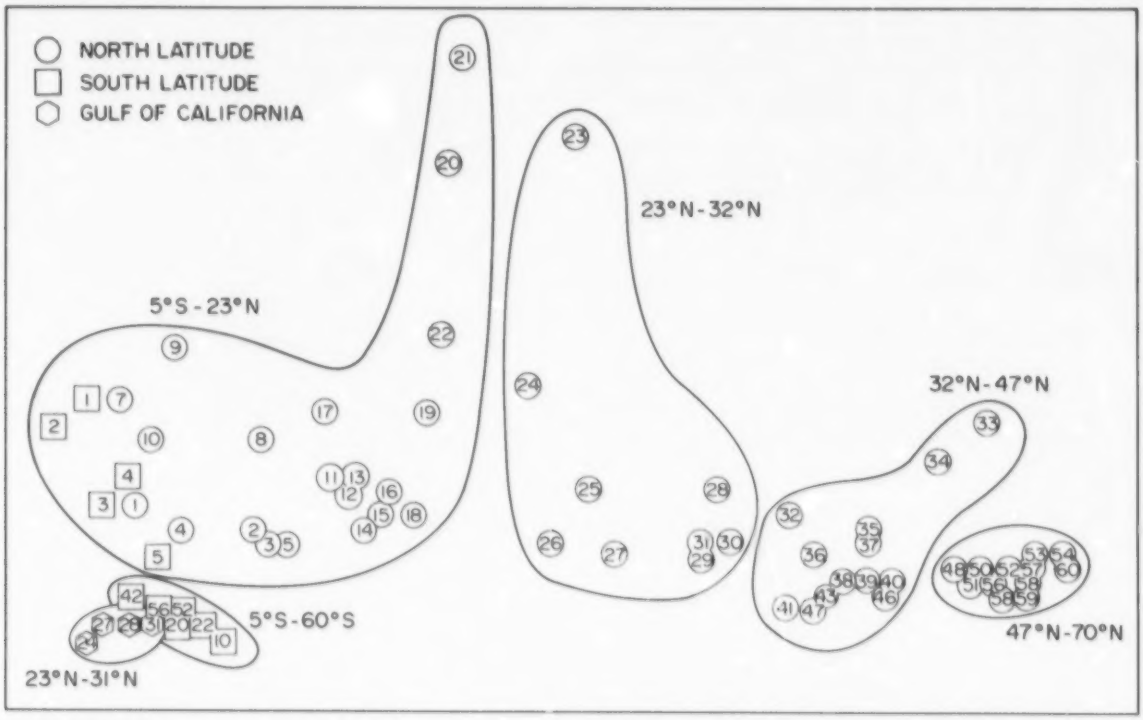

FIG. 22. Principal coordinates analysis of the bivalve fauna of the eastern Pacific Ocean. Plotted points represent one degree blocks of latitude ordinated on the bases of species incidence data combined over all depth zones. Not all blocks have been drawn due to the overlap of coordinates. Enclosing lines are related to results of cluster analyses. The horizontal axis is a function of the number of species present while the vertical axis reflects diversity. Numbers designate latitudinal blocks.

that the California Transition Zone, a region of steep thermal gradients situated adjacent to Point Conception, California (34°N), is carried to depth (Newman 1979). It is axiomatic that boundaries of distribution of individual species will cluster in regions of pronounced environmental change, and such heterogeneity should be less obvious at depth.

Transverse analysis (i.e., between depth intervals) reveals a strong down-slope similarity and merging of the intertidal and subtidal groups (Fig. 23). The shelf fauna shows the highest degree of provincialism; it is the source of the discontinuity at 48°N and the only one with a significant Magellanic element. The slope and abyssal plain group (i.e., 500–1000 m, Fig. 23D) shows a simplification and only a minor element is linked to the tropical fauna. It is apparent that a scheme of province delimitation should include the bathymetric factor, but that depth groups are related. Depth alters the provincial boundaries, which are lost on the deeper shelf, but it is premature to suggest formal depth provinces until these tentative results have been verified and tested on other species groups.

Combining the depth categories (Fig. 23E) yields a boundary pattern agreeing with the major boundaries which have been published over the past one hundred years (Table 4).

Arctic Ocean

The Arctic Ocean is presently well segregated by climate and geography from the Pacific Ocean and, to a lesser extent, the Atlantic Ocean. However, the bivalve fauna comprises only Pleistocene and Recent migrants from adjacent seas (Bernard 1979) and, as already stated, can only be considered a region of recent colonization. The Pacific fauna has played an important role in the colonization of the Arctic basin. Though the timing and extent of Pacific connections is poorly known, it probably existed in the Early Oligocene (Hopkins 1959), although little significant incursion of Pacific elements occurred (Scarlato and Kafanov 1976). Connection with the Atlantic Ocean has been continuous since the Early Tertiary (Eldholme and Thiede 1980). The narrow and shallow Bering Strait is a weak biological barrier and the benthic invertebrate fauna of the Chukchi Sea is principally Pacific (Ushakov 1952; Sparks and Pereyra 1966; Zenkevitch 1963; Stoker 1981) with 45 bivalve species in common (Table 5). The Chukchi Sea is an extension of the northern Bering Sea fauna, and it is the depauperate nature of the latter that has acted as a buffer preventing ingress of more Pacific elements into the Arctic Basin. A number of Pacific species, presently absent from the Arctic Ocean, occur in the northwestern Atlantic and so must have transversed the Arctic. These amphiboreal species (Berg 1918; Nesis 1962) are eurythermal and occur

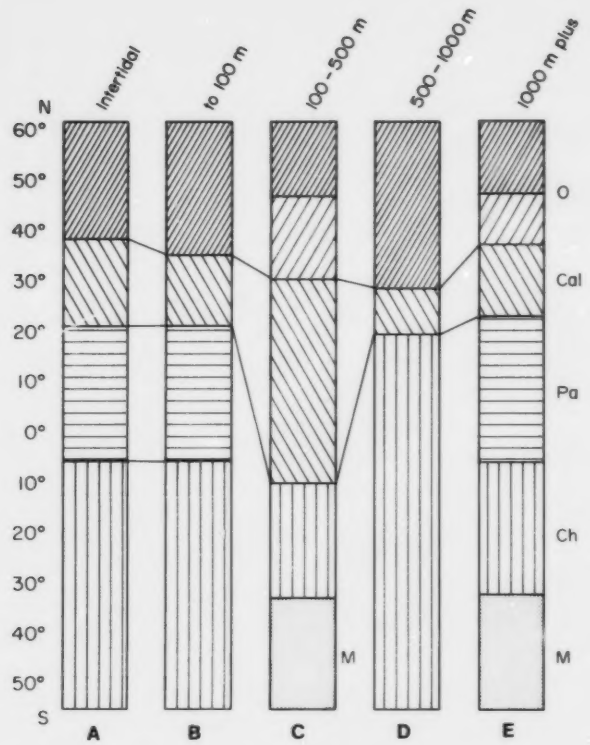

FIG. 23. Transverse analysis of major bivalve faunal zone boundaries of the eastern Pacific Ocean. A, intertidal zone; B, subtidal zone — to 100 m; C, 100–500 m; D, 500–1000 m; E, summary all data. Cal — California, Ch — Chilean, M — Magellanic, O — Oregonian, Pa — Panamic.

in frigid subpolar regions, so their absence from the high Arctic region is difficult to explain. Using the strict amphiboreal criteria, only three bivalve species are so distributed (*Yoldia thraciaermis* (Storer, 1838); *Mactromeris polynyma* (Stimpson, 1860); *Periploma aleuticum* (Krause, 1895) = *P. abyssorum* Bush, 1893), but if we include species extending to the European Atlantic, then *Modiolus modiolus* (Linné, 1758), *Mya arenaria* Linné 1758, and *Macoma obliqua* (Sowerby, 1817) may be added.

The Bering Sea

The Bering Sea includes the wide American continental shelf extending westwards from mainland Alaska to Unimak Island (55°N, 164°E) and then northward to Cape Navarin, USSR (62°N, 180°W), forming an extensive shelf area. The bivalves show little bathymetric separation (Neiman 1963; Haflinger 1981) but are strongly correlated with sediment type (McDonald et al. 1981). While the predominant faunal elements are eastern North Pacific in character (Semenov 1964), with a northward decrease in diversity (Neiman 1963), only one discontinuity is obvious along the Alaskan coast from the Aleutian Archipelago (54°N) to Cape Prince of Wales (66°N), including Bristol Bay, Kuskokwin Bay, and Norton Sound. This is at Nunivak Island (60°N), north of which the Arctic fauna becomes dominant. This marks the northern extent of distribution of Oregonian species, the southern boundary of penetration of Arctic organisms, and the sea-ice boundary. Due to paucity of the fauna, change of only a few species has a strong effect on the analysis, and the discontinuity is chiefly attributable to

TABLE 5. Marine Bivalvia common to the Bering and Chukchi Seas.

Astarte esquimalti (Baird, 1863)
Chlamys pseudislandica MacNeil, 1967
Clinocardium ciliatum (Fabricius, 1780)
Crenella decussata (Montagu, 1808)
Cuspidaria glacialis (G. Sars, 1878)
Cyclocardia crebricostata (Krause, 1885)
Cyrtodaria kurriana Dunker, 1862
Dacrydium vitreum (Moller, 1842 *ex* Holboll MS)
Hiatella arctica (Linné, 1767)
Liocyma fluctuosa (Gould, 1841)
Liocyma viridis Dall, 1871
Lyonsia arenosa (Möller, 1842)
Macoma balthica (Linné, 1758)
Macoma calcarea (Gmelin, 1791)
Macoma loveni (Jensen, 1905 *ex* Steenstrup MS)
Macoma moesta Deshayes, 1855
Musculus corrugatus (Stimpson, 1851)
Musculus discors (Linné, 1767)
Musculus niger (Gray, 1824)
Mya pseudoarenaria Schlesh, 1931
Mya truncata Linne, 1758
Mysella planata (Dall *in* Krause, 1885)
Mysella tumida (Carpenter, 1864)
Mytilus edulis Linné, 1758
Nucula belloti A. Adams, 1856
Nuculana minuta (Fabricius, 1776)
Nuculana pernula (Müller, 1779)
Nuculana radiata (Krause, 1885)
Pandora glacialis Leach *in* Ross, 1819
Panomya ampla Dall, 1898
Panomya arctica (Lamarck, 1818)
Periploma aleutica (Krause, 1885)
Pododesmus macrochisma (Deshayes, 1839)
Portlandia intermedia (M. Sars, 1865)
Portlandia lenticula (Möller, 1842)
Serripes groenlandicus (Bruguière, 1789)
Siliqua alta (Broderip & Sowerby, 1829)
Thracia myopsis Möller, 1842 *ex* Beck MS
Thracia septentrionalis Jeffreys, 1872
Thyasira gouldii (Philippi, 1845)
Tridonta borealis (Schumacher, 1817)
Tridonta montagui (Dillwyn, 1817)
Yoldia hyperborea Torell, 1859 *ex* Loven MS
Yoldia myalis (Couthouy, 1838)
Yoldia scissurata Dall, 1897

failure of further northward penetration of the southern fauna. The southeastern portion of the Bering Sea, particularly near shore, is moderated by the general counterclockwise circulation of the Bering Sea and the entrained Alaskan Current traveling between the Aleutian Islands, bringing in warm Pacific waters. The corresponding shores of Asia are cooled by the southward flowing Oyashio Current, effectively preventing teleplanktic migration and forming a thermal barrier along the shore of Kamchatka Peninsula. The segment of the Bering Sea north of St. Matthew Island to the Gulf of Anadyr is dominated by cold water from the Arctic Ocean and winter sea ice, and faunal diversity is reduced. Few bivalve collections have been made in the region of St. Matthew, St. Lawrence and Nunivak islands. However, the general similarity to the well-known bivalve fauna of the Pribiloff Islands and the absence of endemic species, together with numerous taxa common to the Gulf of Alaska and a paucity of Asian elements, lead us to conclude that the Bering Sea bivalve fauna is an attenuated extension of the Oregonian province, with a relatively weakly demonstrated northern subprovince starting at the latitude of Nunivak Island (60°N).

The western half of the Bering Sea consists of the Aleutian and Komandorskiye Basins separated by the Olyntorskii Ridge. In general, water depth exceeds 3000 m and the benthic fauna is predominantly Asian. The Aleutian Archipelago and the associated Aleutian Trench form the southern boundary of the Bering Sea.

The Gulf of Alaska

The bivalve fauna of the Gulf of Alaska displays little latitudinal variation of diversity, probably the result of the amelioration of oceanographic regimes due to the northward flowing Alaska Current. A few Arctic bivalves persist as relic populations in the deep coastal inlets (e.g. *Portlandia collinsoni* Dall, 1919, *Thracia devexa* G. D. Sars, 1978), but the general fauna is predominantly cold-temperature. The faunal pattern is well-established and even during the Late Oligocene and Early Miocene, it supported few Arctic elements (Allison and Marincovich 1981). The transitory warming periods in the Miocene (Addicott 1970; Douglas and Savin 1971; Addicott et al. 1978) and associated marine transgressions (Tanner 1968) decreased the Asian elements and the region became faunistically fully independent (Watkins 1974). At present, the region is quite distinct from the Japanese fauna. Though some elements migrated westwards during the Pliocene (Kilmer 1978), migrations from the Asian to the American sector predominated (Kafanov 1982). Only 18 bivalves at present have a continuous distribution across the North Pacific, but a significant number exist as discontinuous American and Asian populations (Smith 1904). Also, 84 bivalve species can be recognized as recently descended from a common ancestor, equivalent to the cognate species known from the tropical eastern Pacific Ocean Panamic-Carribean regions (Table 6).

The Oregonian Province

The uniformity of the bivalve fauna extending north from Point Conception, California (34°N), leads us to follow Stephenson and Stephenson (1961) and recognize a single province to the Aleutian Archipelago. We add the eastern Bering Sea to carry the Oregonian Province to the Bering Strait (66°N), though we do recognize an Arctic subprovince from Nunivak Island 60°N through the Bering Strait into the Chukchi Sea. We also recognise a Washingtonian subprovince at Cape Flattery (48°N) based on the distribution of shelf bivalves. This arrangement is more parsimonious than the majority of recent zoogeographic studies, some of which (Valentine 1966) recognize a faunal boundary near Dixon Entrance, British Columbia (54°N). Whereas there does exist a pronounced oceanographic discontinuity (Dodimead and Hollister 1958), it is not reflected in the bivalve distribution. The identification of a faunal boundary at Dixon Entrance may be an artifact introduced by distributional ranges previously thought to terminate at the Aleutian Archipelago, but now known to penetrate the Bering Sea. There is weak faunal discontinuity situated at Kodiak Island, Alaska (58°N), that has no subprovincial significance. While the distribution of bivalves in the entire Oregonian Province is very uniform, except for a general decrease in diversity northwards, there do exist a number of discontinuous distributions which may be significantly clustered between San Francisco, California (38°N), and mid-Oregon (45°N), probably attributable to decrease in habitat niches along these precipitous shores, coupled with strong summer upwelling which reduces summer temperatures. The major faunal discontinuity of the northeastern Pacific Ocean is situated at Point Conception, California, and has been recognized in virtually all marine zoogeographic studies. It is a region of marked change in hydrographic regimes (Reid et al. 1958) where the California Current, the cold southern limb of the Subarctic Current, moves offshore.

The Californian Province

Between Point Conception, California (34°N), south to Bahia Magdalena, Baja California, Mexico (25°N), is situated the well-demarcated Californian Province (Bartsch 1912; Ross 1962), including the coastal islands off the Baja California Peninsula (Los Coronados, Todos Santos, San Martin, San Geronimo, Cedros, Natividad, San Benito, and Asuncion). To the north, the southern Channel Islands off California (San Clemente, Santa Catalina, San Nicolas, and Santa Barbara) and the oceanic Isla de Guadalupe (29°N) are integral parts of this province. The part of the Californian Province along the outer coast of Baja California is a zone of complex faunal patterns, due to intercalated environments with headlands influenced by cold upwelling water containing typical Californian faunal elements, and the protected bays with a distinctly tropical bivalve fauna. This mixed fauna was possibly also influenced by rafting of extraneous elements together with the numerous geologic

TABLE 6. Amphipacific and geminate living Bivalvia.

Northeastern Pacific	Northern Japan
Abra profundorum (E.A Smith, 1885)	,,,
Acharax johnsoni (Dall, 1891)	,,,
Adula californiensis (Philippi, 1847) introduced	*A. schmidti* (Schenck, 1867) *Anomia chinensis* Philippi, 1849.
Astarte alashensis (Dall, 1903)	,,,
Axinopsida viridis (Dall, 1901)	,,,
Bankia setacea (Tryon, 1863)	,,,
Bathyarca corpulenta (E.A. Smith, 1885)	*B. japonica* Habe, 1977.
**Bathyarca nucleator* Dall, 1908	,,,
Calyptogena pacifica Dall, 1891	,,,
**Cardiomya behringensis* Leche, 1883	,,,
Cardiomya pectinata (Carpenter, 1865)	,,,
Chlamys albida (Arnold, 1906)	,,,
Chlamys behringiana (Middendorff, 1849)	,,,
Clinocardium californiense (Deshayes, 1839)	,,,
**Clinocardium ciliatum* (Fabricius, 1780)	,,,
Clinocardium nuttallii (Conrad, 1837)	,,,
Conchocele bisecta (Conrad, 1849)	,,,
Conchocele disjuncta (Gabb, 1866) introduced	,,, *Crassostrea gigas* (Thunberg, 1793).
**Crenella decussata* (Montagu, 1808)	,,,
Crenella divaricata Orbigny, 1847	*C. yokoyama* Nomura, 1922.
Cryptomya californica (Conrad, 1837)	*C. busoensis* Yokoyama, 1922
Cyclocardia crebricostata (Krause, 1895)	,,,
Cyclopecten bistriatus (Dall, 1916)	,,,
Cuspidaria cowani Bernard, 1967	*C. kawamurai* Kuroda, 1940.
Dacrydium vitreum (Möller, 1942)	,,,
Delectopecten randolphi (Dall, 1897)	,,,
Hiatella arctica (Linné, 1767)	,,,
Kellia suborbicularis (Montagu, 1803)	,,,
Limatula subauriculata (Montagu, 1808)	*L. vladivostokensis* Scarlato, 1955.
Liocyma fluctuosa (Gould, 1841)	,,,
Liocyma viridis Dall, 1871	,,,
Lucinoma annulata (Reeve, 1850)	,,,
Lyonsia arenosa (Möller, 1842)	,,,
Lyonsiella parva Okutani, 1962	,,,
**Lyrodus pedicellatus* (Quatrefages, 1849)	,,,
Macoma balthica (Linné, 1758)	*M. takahokoensis* Yamamoto & Habe, 1959.
**Macoma calcarea* (Gmelin, 1791)	,,,
Macoma brota Dall, 1916	,,,
Macoma inquinata (Deshayes, 1855)	M. irus (Hanley, 1845).
Macoma lama Bartsch, 1924	,,,
Macoma nasuta (Conrad, 1837)	*M. tokyoensis* Makiyama, 1927.
Macoma secta (Conrad, 1837)	*M. sectior* (Oyama, 1950).
Mactromeris polynyma (Stimpson, 1860)	,,,
Martesia striata (Linné, 1756)	,,,
Miodontiscus prolongatus Carpenter, 1863 introduced	,,, *Musculista senhousia* (Benson, 1842).
**Musculus corrugatus* (Stimpsdon, 1851)	,,,
**Musculus discors* (Linné, 1763)	,,,
**Musculus niger* (Gray, 1824)	,,,
**Mya arenaria* Linné, 1758	,,,
**Mya truncata* Linné, 1758	,,,

TABLE 6. (Continued)

Mytilus edulis Linné, 1758	introduced
**Nucula bellotti* A. Adams, 1856	"
Nucula tenuis (Montagu, 1808)	"
**Nuculana pernula* (Muller, 1779)	"
Nuttallia nuttallii (Conrad, 1837)	*N. olivacea* (Jay, 1857).
Pandora wardiana (A. Adams, 1859)	"
Panomya ampla Dall, 1898	"
Panomya arctica (Lamarck, 1818)	"
Panomya beringiana Dall, 1916	"
Panope abrupta (Conrad, 1849)	"
**Parvamussium alaskensis* (Dall, 1871)	"
Patinopecten caurinus (Gould, 1850)	*P. yessoensis* (Jay, 1857).
Penitella "kamakurensis" (Yokoyama, 1922)	"
**Peronidia lutea* (Wood, 1828)	"
Pododesmus macroschisma (Deshayes, 1839)	"
Poromya tenuiconcha Dall, 1915	"
Protothaca staminea (Conrad, 1837)	*P. euglypta* (Sowerby, 1914).
Protothaca tenerrima Carpenter, 1857	*P. adamsi* (Reeve, 1863).
Saxidomus nuttalli Conrad, 1837	*S. purpuratus* (Sowerby, 1852)
Septifer bifurcatus (Conrad, 1837)	*S. keeni* Nomura, 1936.
Serripes groenlandicus (Bruguière, 1789)	"
Serripes laperousii (Deshayes, 1839)	"
Siliqua alta (Broderip & Sowerby, 1829)	"
Solen sicarius Gould, 1850	"
Spinula calcar (Dall, 1908)	"
introduced	*Theora fragilis* A. Adams, 1855.
Thyasira gouldii (Philippi, 1845)	*T. tokunagai* Kuroda & Habe, 1951.
introduced	*Trapezium liratum* Reeve, 1843.
Tresus nuttallii (Conrad, 1937)	*T. kennae* (Kuroda & Habe, 1952)
Tridonta alaskensis (Dall, 1903)	"
**Tridonta borealis* Schumacher, 1817	"
Turtonia minuta (Fabricius, 1780)	"
Yoldia amygdalea (Valenciennes, 1846)	"
**Yoldia scissurata* Dall, 1897	"
**Yoldia thraciaeformis* Storer, 1838	"

*Species with continuous distribution.

terrains that constitute the outer edge of the Baja California Peninsula (Smith 1983). The mixed zone extends from Bahia Magdalena (25°N) to the tip of the peninsula at Cabo San Lucas (23°N) and is properly considered a transitional zone (Dawson 1951; Emerson 1956), though it has been accorded provincial status (Hall 1964; Valentine 1966; Brusca and Wallerstein 1979).

The Panamic Province

Cabo San Lucas is the site of the most northerly eastern Pacific coral reef (Brusca and Thomson 1975) and the region where the bivalve fauna becomes recognizable as the Panamic Province, tropical and remarkably uniform to the Golfo de Guayaquil, Ecuador/Peru (3°S). This fauna is carried north into the Gulf of California to at least the latitude of Topolabampo (26°N). The fauna of the Gulf of California has been considered a subprovince (Ekman 1935 as 'subregion') or a distinct province (Briggs 1974). While there is an unexpected degree of endemism of some groups, particularly the crabs (Garth 1960), the fauna as a whole is clearly Panamic. Based on the bivalve data, we follow Dall (1909) and merge it with the Panamic Province. The 1100 km long peninsula of Baja California shields the Gulf of California from the cold Pacific Ocean. Recent work reveals that marine conditions dominated prior to the separation of the Baja California peninsula from the Mexican mainland (Smith 1986). The peninsula has been in position since at least the Pleistocene (Durham and Allison 1960) and the northern portions of the Gulf probably penetrated further north, possibly as far as the San Gorgono Pass, California, reaching to within 80 km of the Pacific coast (Allen 1957). During the Pleistocene, a seaway communicating with the ocean may have existed across the peninsula at the latitude of La Paz (Walker 1960). Such a connection would explain the presence at the head of the Gulf of a small isolated Californian Province fauna which includes at least nine bivalve species (Table 7). There exists no evidence supporting the suggestion (Durham and Allison

TABLE 7. Californian Province Bivalvia present in the Gulf of California.

Americardia biangulata (Sowerby, 1829)
Anomia peruviana Orbigny, 1846
Argopecten circularis (Sowerby, 1835)
**Chama arcana* Bernard, 1976
Chione californiensis (Broderip, 1835)
Chione undatella (Sowerby, 1835)
Chione fluctifraga (Sowerby, 1853)
Crenella divaricata (Orbigny, 1847)
Diplodonta orbella (Gould, 1851)
Ensis myrae Berry, 1953
Leporimetis obesa (Deshayes, 1855)
Limaria hemphilli (Hertlein & Strong, 1846)
**Lucinoma aequizonata* (Stearns, 1891)
Macoma secta (Conrad, 1837)
**Modiolus capax* (Conrad, 1837)
Mytilus edulis Linné, 1758
Nucula declivis Hinds, 1843
**Nutricola tantilla* (Gould, 1853)
**Ostrea conchaphilla* Carpenter, 1857
**Panope globosa* (Dall, 1898) = *P. abrupta*? (Conrad 1849)
**Parvilucina tenuisculpta* (Carpenter, 1864)
Pecten vogdesi Arnold, 1906
**Protothaca staminea* (Conrad, 1837)
Solen rosaceus Carpenter, 1864
Solemya valvulus Carpenter, 1864
**Ventricolaria fordii* (Yates, 1890)

*Isolated species at the head of the Gulf of California.

1960) that these shallow water, cool water organisms migrated around the peninsula during the last thermal minimum.

The Panamic Seaway

It is not possible to undertake a faunal analysis of the Panamic Province in the absence of consideration of the role of the seaway to the Caribbean which existed for a greater part of the history of the eastern Pacific Region and was finally closed by uplift of the Isthmus of Panama $\approx 3.5 \times 10^6$ y.b.p. (Keigwin 1978). Prior to the uplift of the land barrier, there existed an essentially homogenous Tertiary Caribbean Province extending from the tropical West Atlantic to the eastern Pacific Ocean (Woodring 1966, 1974). This common fauna profoundly influenced the development of the fauna of the Panamic Province (Olsson 1972) and in the early Miocene, extended north to at least La Purisima, Mexico (28°N) (Smith 1984). The marked resemblance between the contemporary tropical Pacific Panamic and Caribbean faunas led to postulation of direct connections (Gunther 1868) long before this idea was supported by geological evidence.

The environmental changes associated with closure of the Panamic seaway contributed to significant extinction of the transamerican fauna, so that at present only 22 bivalve species are common to both sides of the Isthmus of Panama (Table 8), representing approximately 2% of the fauna (1% according to Van den Hoek 1975). Speciation has occurred and there exist poorly differentiated species pairs obviously descended from a common ancestor (Middlemiss and Rawson 1971). Vermeij (1978) listed 137 such bivalve pairs, but we recognize 106 cognate pairs; these together with the 22 amphiamerican species, yield a total of 128 pairs, approximately 20% of the Panamic bivalve fauna. The existence of such congeneric species pairs has been needlessly termed paraprovincialism (Petuch 1982). While the majority are descended from populations sundered by the intervening Isthmus of Panama, some may be the product of migrants through minor connecting seaways which persisted some time after the formation of the isthmus (Olsson 1972), or may have formed during the Late Pleistocene interglacial marine transgression (Geister 1977).

The Chilean Province

The southern boundary of the Panamic Province is at Golfo de Guayaquil, Ecuador/Peru (3°S), as recognized by Dall (1909). This is the most northern termination of the southern temperate fauna and is the result of the cold Peru Current sweeping the shore of South America from approximately the latitude of Valparaiso, Chile (33°S), and moving offshore to enter the South Pacific gyral (Posner 1957) at Guayaquil. In the Late Miocene, warmwater species occurred south to 47°S (Zinsmeister 1978), but were extirpated by the establishment of the Peru Current, which displaced thermophilic fauna far northwards.

Though the first comprehensive distributional synopsis of the marine molluscs was by Orbigny (1847), the South American bivalve fauna is relatively poorly known. Our knowledge is based on five lists (Dautzenberg 1896; Dall 1909; Carcelles 1950; Soot-Ryen 1957; Osorio and Bahamonde 1970). In spite of the inadequate basis of information, numerous biogeographic studies have been attempted (Balech 1954; Mann 1954; Semenov 1982). The distribution of the littoral zone fauna was reviewed by Viviani (1975) and Brattstrom and Johnssen (1983) discussed biogeography of numerous invertebrate taxa. However, only Stuardo (1964) dealt exclusively with molluscs. The bivalve fauna of the cool Peruvian and Chilean neritic zones is unexpectedly small, considering the diverse niches available, though clastic substrates are scarce (Orbigny 1845) and upwelling of water with low oxygen saturation may be inimical to faunal development. It is, however remarkably uniform, though several distinct water masses are involved (Sievers and Sandoval 1975), and has been recognized as a single province south to Isla Chiloe, Chile (41°S), the location of an apparent major faunal discontinuity (Dall 1909; Powell 1951; Soot-Ryen 1957; Stuardo 1964; Marincovich 1973) which is not obvious based on our data. It is possible that an unwarranted emphasis has been given to Isla Chiloe as a location of faunal alteration. It is a region of major oceanographic and coastal change and the Golfo Corcovado and Golfo de Ancud, situated between Isla

TABLE 8. Tropical Pacific-Atlantic and cognate species of living Bivalvia.

Tropical Eastern Pacific	Caribbean
Abra tepocana Dall, 1915	*A. lioca* (Dall, 1881)
Americardia guanacastense (Hertlein & Strong, 1947)	*A. media* (Linné, 1758)
Amygdalum pallidulum (Dall, 1916)	*A. sagittatum* (Rehder, 1943)
Anadara biangulata (Sowerby, 1833)	*A. notabilis* (Röding, 1798)
Anadara nux (Sowerby, 1833)	*A. chemnitzi* (Philippi, 1851)
Anatina cyprinus (Wood, 1828)	*A. anatina* (Spengler, 1802)
Arca mutabilis (Sowerby, 1838)	*A. imbricata* Bruguiére, 1789
Arcinella californica (Dall, 1903)	*A. arcinella* (Linné, 1767)
Arcopsis solida (Sowerby, 1833)	*A. adamsi* (Dall, 1886)
Argopecten circularis (Sowerby, 1835)	*A. gibbus* (Linné, 1758)
Atrina maura (Sowerby, 1835)	*A. seminuda* (Lamarck, 1819)
Atrina tuberculosa (Sowerby, 1835)	*A. rigida* (Lightfoot, 1786)
Barbatia gradata (Broderip & Sowerby, 1829)	*B. domingensis* (Lamarck, 1818)
Barnea subtruncata (Sowerby, 1834)	*B. truncata* (Say, 1822)
Botula fusca (Gmelin, 1791)	,,,
Cardiomya costata (Sowerby, 1834)	,,,
Chama frondosa Broderip, 1835	*C. macrophylla* (Gmelin, 1791)
Chione crenifera (Sowerby, 1835)	*C. subrostrata* (Lamarck, 1818)
Chione mariae (Orbigny, 1846)	*C. paphia* (Linné, 1767)
Chione guatulcoensis (Hertlein & Strong, 1948)	*C. mazyckii* Dall, 1902
Codakia distinguenda (Tryon, 1872)	*C. orbicularis* (Linné, 1758)
Condylocardia hippopus (Mörch, 1861)	,,,
Cooperella subdiaphana (Carpenter, 1864)	*C. atlantica* Rehder, 1943
Corbula elenensis (Olsson, 1961)	*C. knoxiana* (C.B. Adams, 1852)
Crassinella adamsi Olsson, 1961	*C. adunca* Weisbord, 1964
Crassinella nuculiformis Berry, 1940	*C. maldonadoensis* (Pilsbry, 1897)
Crassostrea palmula (Carpenter, 1857)	*C. equestris* (Say, 1834)
Crenella divaricata (Orbigny, 1861)	,,,
Ctena galapagana Dall, 1901	*C. orbiculata* (Montagu, 1808)
Cumingia lamellosa Sowerby, 1833	*C. coarctata* Sowerby, 1833
Cyathodonta undulata Conrad, 1849	*C. magnifica* (Jonas, 1850)
Cyclinella singleyi Dall, 1902	*C. tenuis* (Récluz, 1852)
Diplodonta orbella (Gould, 1851)	*D. semiaspersa* Philippi, 1846
Diplothyra curta (Sowerby, 1834)	*D. smithii* Tryon, 1862
Divalinga eburnea (Reeve, 1850)	*D. quadrisulcata* (Orbigny, 1846)
Donax carinatus Hanley, 1843	*D. striatus* Linné, 1767
Donax culter Hanley, 1845	*D. vellicatus* Reeve, 1854
Donax punctatostratus Hanley, 1843	*D. denticulatus* Linné, 1758
Dosinia ponderosa (Schumacher, 1817)	*D. discus* (Reeve, 1854)
Eucrassatella antilarum (Reeve, 1842)	,,,
Fugleria illota (Sowerby, 1833)	*F. tenera* (C.B. Adams, 1845)
Gastrochaena ovata Sowerby, 1834	,,,
Glycymeris lintea Olsson, 1961	*G. spectralis* Nicol, 1952
Gouldia californica Dall, 1917	*G. cerina* (C.B. Adams, 1852)
Gregariella coralliophaga (Gmelin, 1791)	,,,
Gregariella chenui (Récluz, 1842)	,,,
Heterodonax pacificus (Conrad, 1837)	*H. bimaculatus* (Linné, 1758)
Hyotissa hyotis (Linné, 1758)	,,,
Iphigenia altior (Sowerby, 1833)	*I. brasiliana* (Lamarck, 1818)
Isognomon quadratus (Anton, 1837)	*I. bicolor* (C.B. Adams, 1845)
Kellia suborbicularis (Montagu, 1803)	,,,
Laevicardium clarionensis (Hertlein & Strong, 1947)	*L. laevigatus* (Linné, 1758)
Lasaea petitiana (Récluz, 1843)	*L. adamsoni* (Gmelin, 1791)

TABLE 8. (Continued)

Lima tetrica Gould, 1851	*L. lima* (Linné, 1758)
Lithophaga aristata (Dillwyn, 1817)	"
Lopha frons (Linné, 1758)	"
Lucina cancellaris Philippi, 1846	*L. amianta* (Dall, 1901)
Lucina centrifuga (Dall, 1901)	*L. muricata* (Spengler, 1898)
Lyropecten subnodosus (Sowerby, 1835)	*L. nodosus* (Linné, 1758)
Mactrellona subalata (Mörch, 1861)	*M. alata* Spengler, 1802
Malleus regulus (Forskål, 1775)	"
Martesia cuneiformis (Say, 1822)	"
Martesia fragilis Verrill & Bush, 1898	"
Martesia striata (Linné, 1758)	"
Microcardium panamensis (Dall, 1908)	*M. peramabile* (Dall, 1881)
Modiolus americanus (Leach, 1895)	"
Mytella guyanensis (Lamarck, 1819)	"
Mytella striata (Hanley, 1843)	"
Mytilopsis leucophaeta (Conrad, 1831)	"
Nausitora excolpta (Bartsch, 1922)	*N. fusticulosus* (Jeffreys, 1860)
Nucinella subdola (Strong & Hertlein, 1937)	*N. adamsi* (Dall, 1898)
Nuculana hindsii (Hanley, 1860)	*N. acuta* (Conrad, 1831)
Papyridea aspersa (Sowerby, 1833)	*P. soleniformis* (Bruguière, 1789)
Pegophysema edentuloides (Verrill, 1870)	*P. philippiana* (Reeve, 1850)
Periglypta multicostata (Sowerby, 1835)	*P. listeri* (Gray, 1838)
Periploma margariaceum (Lamarck, 1801)	"
Petricola gracilis Deshayes, 1857	*P. pholadiformis* (Lamarck, 1818)
Phlyctiderma discrepans (Carpenter, 1857)	*P. semiasperum* (Philippi, 1836)
Pholas chiloensis Molina, 1782	*P. campechiensis* Gmelin, 1791
Pinctada mazatlanica (Hanley, 1856)	*P. imbricata* Röding, 1798
Pitar alternatus (Broderip, 1935)	*P. circinatus* (Born, 1758)
Pitar lupanaria (Lesson, 1830)	*P. dione* (Linné, 1758)
Plectodon scaber Carpenter, 1864	*P. granulatus* (Dall, 1885)
Plicatula spondylopsis Rochebrunne, 1895	*P. gibbosa* (Lamarck, 1801)
Protothaca asperrima (Sowerby, 1835)	*P. pectorina* (Lamarck, 1818)
Psammotreta aurora (Hanley, 1844)	*P. brevifrons* (Say, 1834)
Pseudochama inermis (Dall, 1871)	*P. radians* (Lamarck, 1819)
Pteria sterna (Gould, 1851)	*P. colymbis* (Röding, 1798)
Raeta undulata (Gould, 1851)	*R. plicatella* (Lamarck, 1818)
Sanguinolaria bertini Pilsbry & Lowe, 1932	*S. cruenta* (Lightfoot, 1786)
Sanguinolaria ovalis Reeve, 1857	*S. sanguinolenta* (Gmelin, 1791)
Semele guaymasensis Pilsbry & Lowe, 1932	*S. anteriocosta* (Vokes, 1938)
Semele lenticularis (Sowerby, 1833)	*S. proficua* (Pulteney, 1799)
Semele pacifica Dall, 1915	*S. bellastriata* (Conrad, 1837)
Semele venusta (Reeve, 1953)	*S. casali* (Doello-Jurado, 1949)
Solecurtus guaymasensis Lowe, 1935	*S. cumingianus* Dunker, 1861
Solen rudis C.B. Adams, 1852	*S. obliquus* Spengler, 1794
Sphenia luticola (Valenciennes, 1846)	*S. antillensus* Dall & Simpson, 1901
Spondylus princeps Broderip, 1833	*S. americanus* Hermann, 1781
Strigilla chroma Salisbury, 1934	*S. pseudocarnaria* Boss, 1967
Strigilla ervilia (Bartsch, 1922)	*S. producta* Tryon, 1870
Strigilla disjuncta Carpenter, 1856	*S. gabbi* Olsson & McGinty, 1958
Tangelus affinis (C.B. Adams, 1852)	*T. plebius* (Lightfoot, 1786)
Tellina amianta Dall, 1900	*T. sybaritica* Dall, 1881
Tellina cumingii Hanley, 1844	*T. listeri* Röding, 1798
Tellina eburnea Hanley, 1844	*T. angulosa* Gmelin, 1791
Tellina esmeralda (Olsson, 1961)	*T. sandix* Boss, 1968

TABLE 8. (Continued)

Tellina fluctigera Dall, 1908	*T. persica* Dall & Simpson, 1901
Tellina hiberna Hanley, 1844	*T. gibber* Ihering, 1907
Tellina laceridens Hanley, 1844	*T. alternata* Say, 1822
Tellina lyra Hanley, 1844	*T. juttingae* Altena, 1965
Tellina meropsis Dall, 1900	*T. mera* Say, 1834
Tellina ochracea Carpenter, 1864	*T. laevigata* Linné, 1750
Tellina pacifica Dall, 1900	*T. americana* Dall, 1906
Tellina pristiphora Dall, 1900	*T. squamifera* Deshayes, 1855
Tellina reclusa Dall, 1900	*T. aequistriata* Say, 1824
Tellina rhynchoscuta (Olsson, 1961)	*T. cristallina* Spengler, 1798
Tellina simulans C.B. Adams, 1852	*T. punicea* Born, 1778
Tellina subtrigona Sowerby, 1866	*T. exerythra* Boss, 1964
Tellina suffusa Dall, 1900	*T. tampaensis* Conrad, 1866
Tellina ulloana Hertlein, 1968	*T. declivis* Sowerby, 1868
Tellina virgo Hanley, 1844	*T. iris* Say, 1822
Tellidora burnetti (Broderip & Sowerby, 1829)	*T. cristata* (Récluz, 1842)
Tivella byronensis (Gray, 1838)	*T. mactroides* (Born, 1778)
Trachycardium consors (Sowerby, 1833)	*T. isocardia* (Linné, 1758)
Trachycardium senticosum (Sowerby, 1833)	*T. muricatum* (Linné, 1758)
Ventricolaria isocardia (Verrill, 1870)	*V. rigida* (Dillwyn, 1817)
Verticordia ornata (Orligny, 1853)	,,,

Chiloe and the mainland, experience reduced salinity (Dahl 1960) which may be an effective barrier for some organisms (Leloup 1956; Madsen 1956; Garth 1957; Knox 1960). It is also a region of topographic change, the shorelines to the north being mostly straight, while to the south they are broken by numerous fjords and islands. More importantly, Isla Chiloe is the latitude of divergence of the Subantarctic Current into the northward flowing Peru Current and the southward flowing Cape Horn Current. In spite of the conjunction of all these environmental factors, except for the general poleward decreasing diversity, the bivalve fauna is remarkably uniform and we prefer to recognize the whole region as the Chilean Province, with no Peruvian Province because of the Peruvian warmwater bivalve fauna in Panama. As previously stated, the number of bivalve species occurring in Chile is rather small. This trend is also shown in Pliocene and Pleistocene assemblages, which demonstrate significant impoverishment, particularly of Atlantic elements with the development of Pacific species (Herm 1969).

The South American shelf zone fauna is related to that of Antarctic, New Zealand and Australia, as evidenced by the wide distribution of some molluscs (Sohl 1977; Crame 1983) and other organisms (Allan 1963). We have already commented on this similarity and it is likely that an isthmus connected the tip of South America to Antarctica and that Drake Passage opened less than 30 $\times$ 10^6 y.b.p. (Craddock and Hollister 1976).

The Magellanic Subprovince

We propose a significant departure from previous studies by according subprovincial status only to the Magellanic region, situated south of Isla Chiloe to Cabo de Hornos and extending in attenuated form into the South Atlantic Ocean. Our data support integration with the Chilean province, but with a Magellanic incursion of the shelf and slope bivalves to Valparaiso, Chile (32°S). Ten species of bivalves are known to extend to Argentina and the Falkland Islands (Table 9), including the very widely distributed mussel *Gaimardia trapesina* (Lamarck, 1819), which also occurs in New Zealand. *Aulacomya ater* (Molina, 1782) is probably identical to the New Zealand *A. maoriana* (Iredale, 1915). The oyster genus *Tiostrea* occurs both in South America and New Zealand.

TABLE 9. Living Magellanic Bivalvia extending to the south Atlantic Ocean (Tierra del Fuego and Islas Malvinas).

Aulacomya ater (Molina, 1782)
Astarte longirostra Orbigny, 1846
Barnea lamellosa (Orbigny, 1846)
Brachidontes purpuratus (Lamarck, 1819)
Cyclopecten vitreus (Gmelin, 1791)
Ensis macha (Molina, 1782)
Gaimardia trapesina (Lamarck, 1819)
Hiatella solida (Sowerby, 1834)
Mulinia edulis (King & Broderip, 1832)
Mytilus chilensis Hupé, 1854

The Offshore Oceanic Islands

The oceanic islands of the eastern Pacific Ocean are defined as those terrestrial bodies situated off the American continental shelf. They comprise only eight groups, all of volcanic origin associated with the margins of crustal plates (Fig. 24). Situated varying distances off the mainland, these islands are all separated by deep water and their marine fauna has originated either by migration or local evolution, though there exists evidence that some islands, at least, were connected to the mainland or that there once existed intermediary islands that have since disappeared. The marine fauna of the majority of islands is poorly known and deserves more research, as the islands as a whole present an important opportunity for the study of island biogeography and the development of insular faunas.

Based on present information of the bivalve fauna, oceanic islands of the eastern Pacific Ocean are not related to the nearest islands of the Indo-Pacific region. However, as some western Pacific elements are established, particularly in groups other than the bivalves, it is necessary to consider faunal relationships to their nearest neighbours, the Hawaiian Archipelago and Isla de Pascua (Easter Island).

FIG. 24. Locations of the oceanic islands of the eastern Pacific Ocean.

The Hawaiian Group

The Hawaiian group of islands is a linear volcanic chain which emerged during the Cretaceous (Menard and Hamilton 1963) approximately 103 × 10^6 y.b.p. The fauna can only have become established since the Miocene (Menard et al. 1962; Ladd et al. 1967). This is possibly the most isolated insular fauna known but is distinctly Indo-Pacific in character (Ekman 1953). The bivalves have been reviewed by Dall et al. (1938) and monographed by Kay (1979). As in the cases of several Indo-Pacific islands (Kay 1967), bivalves are proportionately poorly represented, possibly due to a lack of habitat diversity. Based on these published reports and research of various collections, including a survey and review of the collection of the Bernice P. Bishop Museum, Honolulu, we estimate the total number of bivalves to be 150 species, of which 37% are endemic but rather closely related to wide ranging Indo-Pacific species. Some 61% of the bivalve fauna comprises Indo-Pacific species and only three species are present on the American continent (Table 10).

TABLE 10. Marine Bivalvia living in the Hawaiian Islands.

Aequipecten superbus (Sowerby, 1842)
* *Allogrāma oahuensis* (Dall, 1913)
* *Amygdalum newcombi* Dall, Bartsch & Rehder, 1938
Anisodonta angulata H. Adams, 1870
Anisodonta recluzii (A. Adams, 1864)
Anomia nobilis Reeve, 1859
* *Anomia tyria* Reeve, 1859
* *Arca kauaia* (Dall, Bartsch & Rehder, 1938)
Arca ventricosa Lamarck, 1819
* *Argopecten loxoides* Sowerby, 1842
Atrina vexillus (Born, 1778)
Bankia bipalmulata (Lamarck, 1801)
Barbatia alia (Dall, Bartsch & Rehder, 1938)
Barbatia decussata (Sowerby, 1823)
Barbatia divaricata (Sowerby, 1833)
Barbatia lima (Reeve, 1844)
* *Barbatia molokaia* Dall, Bartsch & Rehder, 1938
Barbatia nuttingi (Dall, Bartsch & Rehder, 1938)
Barbatia rectangula (Dall, Bartsch & Rehder, 1938)
Barbatia tenella Reeve, 1844
Babatia hiloa Dall, Bartsch & Rehder, 1938
Bathyarca asperula (Dall, 1881)
Botula silicula (Lamarck, 1819)
Brachidontes crebristriatus (Conrad, 1837)
Cadella semen (Hanley, 1844)
Cardita aviculina Lamarck, 1819
Cardita thaanumi Dall, Bartsch & Rehder, 1938
* *Cardita excisa* Philippi, 1847
* *Carditella hawaiensis* Dall, Bartsch & Rehder, 1938
Chama iostoma Conrad, 1837
* *Chlamys alli* Dall, Bartsch & Rehder, 1938
Chlamys coruscans (Hinds, 1845)
* *Chlamys irregularis* (Sowerby, 1842)

TABLE 10. (Continued)

Chlamys hawaiensis Dall, Bartsch & Rehder, 1938
Codakia punctata Linné, 1758
Crassostrea gigas (Thunberg, 1793)†
Crassostrea virginica (Gmelin, 1791)†
Crassostrea sandvicensis Sowerby, 1871
Ctena bella (Conrad, 1837)
Ctena transversa Dall, Bartsch & Rehder, 1938
Cuspidaria hawaiensis Dall, Bartsch & Rehder, 1938
Cuspidaria pailoloana Dall, Bartsch & Rehder, 1938
Decatopecten noduliferum (Sowerby, 1842)
Dimya mimula Dall, Bartsch & Rehder, 1938
Dimya molokaia Dall, Bartsch & Rehder, 1938
Dorisca nana (Melvill, 1898)
Dysmea tongana (Quoy & Gaimard, 1834)
Euciroa pacifica (Dall, 1895)
Fragrum mundum (Reeve, 1845)
Gastrochaena cuneiformis Spengler, 1783
Gastrochaena cymbium Spengler, 1783
Gastrochaena oakuana Dall, Bartsch & Rehder, 1938
Glycymeris arcodentiens (Dall, 1895)
Glycymeris diomedea Dall, Bartsch & Rehder, 1938
Glycymeris molokaia Dall, Bartsch & Rehder, 1938
Glycymeris nux Dall, Bartsch & Rehder, 1938
Grammatomya kanaka (Pilsbry, 1921)
Halicardia gouldi Dall, Bartsch & Rehder, 1938
Hiatella solida (Sowerby, 1934)
Hitia ovalis Dall, Bartsch & Rehder, 1938
Isognomon californicus (Conrad, 1837)
Isognomon incisum (Conrad, 1837)
Isognomon legumen (Gmelin, 1791)
Isognomon perna (Linné, 1767)
Jouannetia cumingii (Sowerby, 1849)
Kellia porculus Pilsbry, 1904
Kellia rosea Dall, Bartsch & Rehder, 1938
Kona symmetrica (Pilsbry, 1921)
+ *Lasaea petitiana* (Récluz, 1843)
Leiochasmea elongata Preston, 1903
Leiochasmea thaanumi (Pilsbry, 1931)
Lima hawaiana Dall, Bartsch & Rehder, 1938
Lima lakaina Dall, Bartsch & Rehder, 1938
Lima parallela Dall, Bartsch & Rehder, 1938
Limaria basilanica (Adams & Reeve, 1850)
Limopsis waikikia Dall, Bartsch & Rehder, 1938
Lioconcha hieroglyphica (Conrad, 1837)
Lithophaga fasciola Dall, Bartsch & Rehder, 1938
Lithophaga hawaia Dall, Bartsch & Rehder, 1938
Lonoa hawaiensis Dall, Bartsch & Rehder, 1938
Lucina edentula (Linné, 1758)
Lyrodus affinis (Deshayes, 1863)
Lyrodus medilobata (Edmondson, 1942)
Lyrodus pedicillatus (Quatrefages, 1849)
Macoma dispar (Conrad, 1837)
Macoma clathrata (Deshayes, 1835)
Mactra thaanumi Dall, Bartsch & Rehder, 1938
+ *Malleus regulus* (Forskål, 1775)

TABLE 10. (Continued)

+ *Martesia striata* (Linné, 1758)
Meiocardia hawaiana Dall, Bartsch & Rehder, 1938
Mirapecten mirificus (Reeve, 1853)
Modiolus matris (Pilsbry, 1921)
Modiolus difficilis (Deshayes, 1863)?
Musculus aviarius Dall, Bartsch & Rehder, 1938
Myonera dispar Dall, Bartsch & Rehder, 1938
Memocardium thaanumi (Pilsbry, 1921)
Nesobornia bartschi Chavan, 1969
Nucula hawaiensis Pilsbry, 1921
Ostrea hanleyana Sowerby, 1871
Ostrea laysana Dall, Bartsch & Rehder, 1938
Ostrea lima Sowerby, 1871
Parvamussium diomedeum Dall, Bartsch & Rehder, 1938
Parvamussium kauaium Dall, Bartsch & Rehder, 1938
Parvamussium molokaium Dall, Bartsch & Rehder, 1938
Parvamussium nesiotum Dall, Bartsch & Rehder, 1938
Parvamussium pailoloum Dall, Bartsch & Rehder, 1938
Pecten diomedeus Dall, Bartsch & Rehder, 1938
Periglypta reticulata (Linné, 1758)
Pillucina hawaiiensis (E.A. Smith, 1885)
Pillucina spaldingi (Pilsbry, 1921)
Pinctada margaritifera (Linné, 1758)
Pinctada radiata (Leach, 1814)
Pinguitellina pinguis (Hanley, 1845)
Pinna bicolor Gmelin, 1791
Pinna muricata Linné, 1758
Policordia diomedea Dall, Bartsch & Rehder, 1938
Poromya transversa Dall, Bartsch & Rehder, 1938
Promantellum fragilis (Gmelin, 1791)
Pteria penguin (Röding, 1798)
Radobornia bryani (Pilsbry, 1921)
Rochefortina sandwichensis (E.A. Smith, 1885)
Scintilla philippinensis Deshayes, 1856
Scintillona stigmatica (Pilsbry, 1921)
Semele australis (Sowerby, 1832)
Semelangulus crebrimaculatus (Sowerby, 1867)
Septifer bilocularis (Linné, 1758)
Septifer rudis Dall, Bartsch & Rehder, 1938
Solecurtus baldwini Dall, Bartsch & Rehder, 1938
Spondervilia bisculpta (Gould, 1861)
Spondylus hystrix Röding, 1798
Spondylus linguafelis Sowerby, 1847
Spondylus tenebrosus Reeve, 1856
Stenolena hawaiensis Dall, Bartsch & Rehder, 1938
Streptopinna saccata (Linné, 1758)
Tapes philippinarum (Adams & Reeve, 1850)†
Tellina crucigera Lamarck, 1818
Tellina elizabethae Pilsbry, 1918
Tellina palatum Iredale, 1929
Tellina perna (Spengler, 1798)
Tellina robusta (Hanley, 1844)
Tellinides ovalis Sowerby, 1867
Teredo bartschi Clapp, 1923
Teredo clappi Bartsch, 1923

TABLE 10. (Continued)

Teredo furcifera Martens *in* Semon, 1894
Teredo princesae Sivickis, 1928
Teredo triangularis Edmondson, 1942
Terua crypta Dall, Bartsch & Rehder, 1938
Terua pacifica Dall, Bartsch & Rehder, 1938
Ventricolaria toreuma (Gould, 1850)

* Endemic species.
† Introduced.
+ Also on American continent.

Isla de Pascua

Isla de Pascua (Easter Island) and the associated Isla Sala y Gomez (Fig. 24) mark the southeastern boundary of the Indo-Pacific region. These two widely separated islands lie on the formative edge of the Nazca Plate, which is being subducted along the west coast of South America, and are connected to Islas San Felix and San Ambrosia by a series of seamounts. However, they are faunally associated with the Indo-Pacific. The bivalve fauna is poorly known, but appears to be sparse. The initial list published (Dall 1908) included only five species, no additions appeared in Fuentes (1914), while Odhner (1922) listed only one bivalve species. Lamy (1936, 1938) recorded three bivalves and Steele (1957) augmented it to six species. All these records were based on beach drift material, but are unexpectedly few. The most comprehensive treatment (Rehder 1980) recognizes 14 bivalves. Castilla and Rozbaczylo (1987) discuss molluscs. Fully 79% of the fauna is Indo-Pacific and two species, the Panpacific *Lasaea petitiana* Récluz, 1843, and *Hiatella solida* (Sowerby, 1842), extend to continental America (Table 11). There is a record of *Arca angulata* King & Broderip, 1831, known from Islas Juan Fernandez and San Felix, found in a piece of pumice, but the species is apparently not established. Similarly, a single valve of the mainland South American *Chlamys patagonicus* (King & Broderip, 1831), reported by Steele (1957), is doubtless adventitious (Rehder 1980). Frequently considered a distinct province, Rehder (1980) thought the molluscan fauna to bear a close relationship to Hawaii and only secondarily to Polynesia, as suggested by Schilder (1965).

TABLE 11. Marine Bivalvia living in Isla de Pascua.

Barbatia cf. *nuttingi* (Dall, Bartsch & Rehder, 1938)
Cadella semen (Hanley, 1844)
Chama iostoma Conrad, 1837
**Chlamys pasca* (Dall, 1908)
Codakia bella (Conrad, 1837)
Hiatella solida (Sowerby, 1834)
Lasaea petitiana Récluz, 1843
Lima sp.
Malleus maculosus Reeve, 1843
Modiolus matris Pilsbry, 1921
**Nucula polynesia* Rehder, 1980
Promantellum fragilis (Gmelin, 1791)
Semele australis (Sowerby, 1833)
Septifer bryana (Pilsbry, 1921)
Tellina mauia (Dall, Bartsch & Rehder, 1938)

*Endemic species.

The American Islands

We will now review the bivalve fauna of the American oceanic islands from north to south. The northernmost Isla de Guadalupe (29°N), lying approximately 225 km off the coast of Baja California, Mexico, supports a well-known bivalve fauna (Strong and Hanna 1938a, 1938b; Strong 1954; Chace 1958). Including new material deposited in the Los Angeles County Museum of Natural History, 22 bivalves are known (Table 12), the small number due to the precipitous shoreline with little variety of habitat and almost total lack of clastic infaunal sites. The species listed are nearly all members of the Californian Province, the cool offshore waters favouring the establishment of northern outriders frequently absent form the adjacent mainland shore. No endemic or Indo-Pacific elements are present, and the fauna is considered to be an integral portion of the Californian Province.

TABLE 12. Marine Bivalvia living in Isla de Guadalupe.

Adula diegensis (Dall, 1911)
Arcopsis solida (Sowerby, 1833)
Barbetia bailyi (Bartsch, 1931)
Chama arcana Bernard, 1976
Chlamys gigantea (Gray, 1825)
Crenella divaricata (Orbigny, 1847)
Cyclopecten pernomus (Hertlein, 1935)
Glycymeris guadalupensis Strong, 1938
Grippina californica Dall, 1912
Hiatella arctica (Linné, 1767)
Lasaea subviridis Dall, 1899
Leptopecten latiauratus (Conrad, 1837)
Lucina californica Conrad, 1837
Megacrenella columbiana (Dall, 1897)
Milneria kelseyi Dall, 1916
Parvamussium alaskense (Dall, 1872)
Pecten diegensis Dall, 1898
Philobrya setosa (Carpenter, 1864)
Pododesmus pernoides (Gray, 1853)
Psephidia cymata Dall, 1913
Tellina carpenteri Dall, 1900
Transenella pannosa (Sowerby, 1835)

Islas de Revillagigedo

The Islas de Revillagigedo, a group of small islands (Fig. 24) situated on the Clarion Fracture Zone (18°N), comprising Islas Clarion, Socorro, San Benedicto, and Roca Partida, are located approximately 400 km south of Cabo San Lucas, Baja California, Mexico. The two major islands are separated by more than 350 km of water more than 3500 m deep, but collecting surveys are not sufficiently comprehensive to detect faunal differences, so they are treated as a single unit. The bivalve fauna is little known and collecting has been sporadic and

undirected. Strong and Hanna (1938b) recorded only six bivalves; however, review of materials deposited in the Los Angeles County Museum brings the total to 29 species, chiefly Panamic, but as noted by Dall (1916), a few Californian elements persist (Table 13). No endemic species are known and the fauna is exclusively West American. Twenty-one species extend to the other American oceanic islands. We conclude that the Islas de Revillagigedo are an integral portion of the Panamic Province.

TABLE 13. Marine Bivalvia living in the Islas de Revillagigedo.

Anadara multicostata (Sowerby, 1833)
Anomia peruviana Orbigny, 1846
Arca pacifica (Sowerby, 1833)
Arcopsis solida (Sowerby, 1833)
Argopecten circularis (Sowerby, 1835)
Barbatia baileyi (Bartsch, 1931)
Cardites laticostata (Sowerby, 1833)
Chione undatella (Sowerby, 1835)
Chlamys lowei (Hertlein, 1935)
Codakia distinguenda (Tryon, 1872)
Ctena mexicana (Dall, 1901)
Cyclopecten pernomus (Hertlein, 1935)
Diplodonta subquadrata Carpenter, 1856
Dosinia dunkeri (Philippi, 1844)
Gastrochaena ovata Sowerby, 1834
Glycymeris inaequalis (Sowerby, 1833)
Lithophaga aristata (Dillwyn, 1817)
Lithophaga calyculata (Carpenter, 1857)
Lucina lampra (Dall, 1901)
Lyropecten subnodosus (Sowerby, 1835)
Modiolus capax (Conrad, 1837)
Mytilus californianus (Conrad, 1837)
Pecten sericeus Hanley, 1845
Penitella penita (Conrad, 1837)
Semele craneana Hertlein & Strong, 1949
Septifer zeteki Hertlein & Strong, 1946
Spondylus calcifer Carpenter, 1857
Tellina ochracea Carpenter, 1864
Transennella modesta (Sowerby, 1835)

Île Clipperton

Île Clipperton (10°N) is situated approximately 1000 km southwest of Cabo Corrientes, Mexico (Fig. 24). It is the most westerly of the islands associated with the American continental plate. It comprises an atoll with an encircling coral reef. The marine fauna has received much attention and is perhaps the best known insular fauna of the eastern Pacific Ocean (Bartsch and Rehder 1939; Hertlein and Emerson 1953; Hertlein and Allison 1966; Salvat and Ehrhardt 1970; Salvat and Salvat 1972). Twenty bivalve species are recorded, including one endemic species and five extending to the Indo-Pacific region (Table 14). Unlike the gastropods which are strongly Indo-Pacific in relationship, 85% of the bivalves are clearly West American and the fauna is definitely assignable to the Panamic Province. There are a significant number of Indo-Pacific elements, possibly transported across the Pacific Ocean with the eastward summer flow of the Equatorial Counter Current, while the American contribution to the fauna is carried by the winter flow off the American shore (Fig. 25).

TABLE 14. Marine Bivalvia living at Île Clipperton.

Anomia peruviana Orbigny, 1846
Arca mutabilis (Sowerby, 1833)
Barbatia divaricata (Sowerby, 1833)
Barbatia reeveana (Orbigny, 1846)
Chama squamuligera Pilsbry & Lowe, 1932
Codakia distinguenda (Tryon, 1872)
Codakia punctata (Linné, 1758)
**Ctena clippertonensis* Bartsch & Rehder, 1939
Cyclopecten zacai (Hertlein, 1935)
Gastrochaena ovata Sowerby, 1834
Hyotissa hyotis (Linné, 1758)
Isognomon janus Carpenter, 1857
Isognomon quadratus (Anton, 1837)
Lithophaga calyculata (Carpenter, 1856)
Lithophaga hancocki Soot-Ryen, 1955
Lithophaga plumula Hanley, 1843
Martesia striata (Linné, 1758)
Pinctada mazatlanica (Hanley, 1856)
Pinna rugosa Sowerby, 1835
Spondylus linguaefelis Sowerby, 1847

* Endemic species.

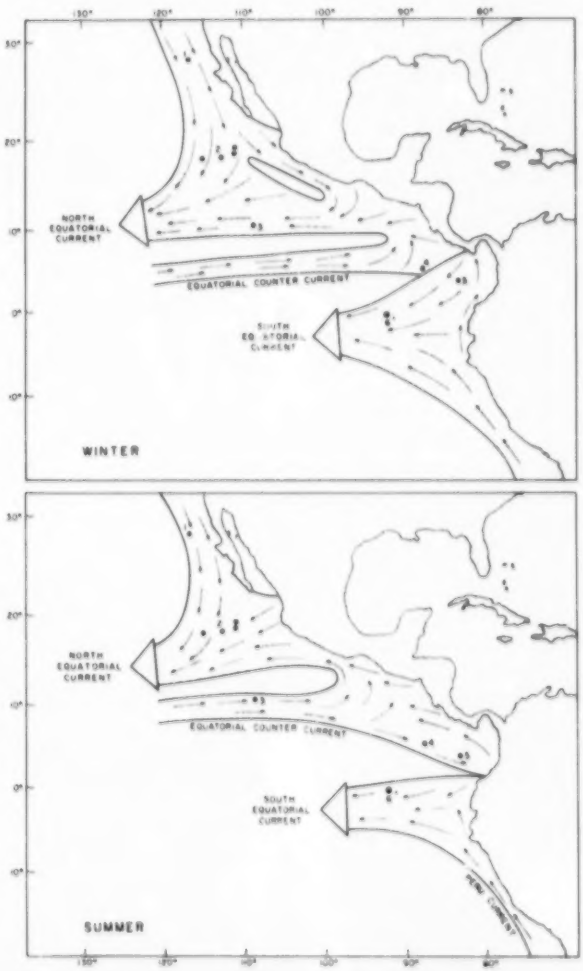

FIG. 25. Surface currents in summer and winter around the oceanic islands of the tropical eastern Pacific Ocean (modified from Wyrtki 1965). 1 = Isla de Guadalupe, 2 = Islas de Revillagigedo, 3 = Île Clipperton, 4 = Isla del Coco, 5 = Isla de Malpelo, 6 = Archipiélago de Colón.

Isla del Coco

Isla del Coco, situated at 6°N (Fig. 24), some 500 km west of Costa Rica, carries some suggestion that it may have been part of a westward peninsula extending off Costa Rica during the Miocene (Vinton 1951). The molluscan fauna was, until recently, almost unknown (Biolley 1907, 1935; Hertlein 1932; Emerson 1967). Montoya (1983) included only 16 species of bivalves. Materials collected by the Allan Hancock Pacific Expeditions, now in the Los Angeles County Museum of Natural History, and by D.R. Shasky, presently in the Santa Barbara Museum, increase the fauna to 38 species. The efforts of Montoya and his associates (M. Montoya, P.O. Box 6327, San Jose, Costa Rica, pers. comm.) have expanded the known bivalve fauna to 80 species and we have included their additional records (Table 15). No endemic species are present and only seven are Indo-Pacific. Some 84% of the fauna is West American, and 70% of the bivalves are present on some of the other American oceanic islands. The record of Emerson (1978) of *Isognomon quandrangularis* (Reeve, 1858) is probably referable to *I. quadratus* (Anton, 1837), a common species of the West Pacific region. *Lopha folium* (Linne, 1758) is cosmopolitan in distribution, while both *Isognomon incisum* (Conrad, 1837) and *Cardita aviculina* Lamarck, 1819, are also Indo-Pacific. Isla del Coco is subject to an ocean current regime similar to that experienced by Île Clipperton, and in winter receives the eastward flow of the Equatorial Counter Current (Fig. 25). The relative proximity of the American continent, and the increased distance to be crossed by Indo-Pacific teleplanktonic larvae, may explain the poor representation of West Pacific elements compared to those of Île Clipperton. We consider Isla del Coco to be part of the Panamic Province.

TABLE 15. Living Marine Bivalvia occurring at Isla del Coco.

•*Americardia guanacastensis* (Hertlein & Strong, 1947)
•*Amerycina colpoica* (Dall, 1913)
Anadara grandis (Broderip & Sowerby, 1839)
Anadara multicostata (Sowerby, 1833)
Anadara rheinharti (Lowe, 1833)
Anomia peruviana Orbigny, 1846
Arca mutabilis (Sowerby, 1833)
•*Arca pacifica* (Sowerby, 1833)
Arcopsis solida (Sowerby, 1833)
Argopecten circularis (Sowerby, 1835)
•*Atrina tuberculosa* (Sowerby, 1835)
•*Barbatia gradata* (Broderip & Sowerby, 1829)
•*Barbatia reeveana* (Orbigny, 1846)
Cardita aviculina Lamarck, 1819+
Cardites laticistata (Sowerby, 1833)
•*Chama squamuligera* Pilsbry & Lowe, 1932
•*Codakia distinguenda* (Tryon, 1872)
•*Condylocardia hippopus* (Mörch, 1861)
•*Corbula esmeralda* Olsson, 1961
•*Corbula porcella* Dall, 1916
Crenella divaricata (Orbigny, 1843)

TABLE 15. *(Continued)*

•*Ctena clarionensis* Hertlein & Strong, 1946
Cyclopecten cocosensis (Dall, 1908)
Cyclopecten exquisitus Grau, 1959
•*Cymatioa eletris* (Berry, 1963)
Diplodonta subquadrata Carpenter, 1856
•*Divalinga eburnea* (Reeve, 1850)
•*Divalinga perparvula* (Dall, 1901)
Gastrochaena rugulosa Sowerby, 1834
•*Glycymeris inaqeualis* (Sowerby, 1833)
•*Glycymeris lintea* Olsson, 1961
Glycymeris multicostata (Sowerby, 1833)
•*Glycymeris strigilata* (Sowerby, 1833)
•*Gouldia californica* Dall, 1917
•*Gregariella coralliophaga* (Gmelin, 1791)
•*Haliris aequacostata* (Howard, 1950)
•*Halodakra subtrigona* (Carpenter, 1857)
Hyotissa solida (Sowerby, 1871)
•*Isognomon incisum* (Conrad, 1837)+
Isognomon quadratus (Anton, 1837)+
Lima tetrica Gould, 1851
•*Limatula similaris* (Dall, 1917)
Limopsis dalli (Lamy, 1912)
Lithophaga aristata (Dillwyn, 1817)
•*Lithophaga calyculata* (Carpenter, 1857)
•*Lithophaga plumula* (Hanley, 1844)
Lithophaga peruviana (Orbigny, 1846)
Lopha folium (Linné, 1758)+
Lyropecten subnodosus (Sowerby, 1835)
Malleus regulus (Forskål, 1775)+
•*Papyridea aspersa* (Sowerby, 1833)
Pecten hancocki Grau, 1959
Pecten perulus Olsson, 1961
Pecten sericeus Hinds, 1845
Pecten vogdesi Arnold, 1906
•*Plectodon scaber* Carpenter, 1864
•*Pinctada mazatlanica* (Hanley, 1856)
•*Pitar hertleini* Olsson, 1961
•*Plicatulla spondylopsis* Rochebrune, 1895
•*Promantellum pacifica* (Orbigny, 1846)
Poromya scapha (Dall, 1902)
•*Pseudochama clarionensis* Willett, 1938
Pteria sterna (Gould, 1851)
•*Saccostrea palmula* (Carpenter, 1857)
•*Semele formosa* (Sowerby, 1833)
•*Semele purpurascens* (Gmelin, 1791)
Semele rupium (Sowerby, 1833)
Septifer zeteki Hertlein & Strong, 1946
•*Solecardia eburnea* Conrad, 1849
Spondylus linguaefelis Sowerby, 1847
•*Spondylus nicobaricus* Schreiber, 1793+
•*Steptopinna saccata* (Linné, 1758)+
•*Strophocardia megastropha* (Gray, 1825)
Striostrea prismatica (Gray, 1825)
Tellina sp. indent
•*Tellina coani* Keen, 1971
•*Tellina cumingii* Hanley, 1844
•*Tellina ochracea* Carpenter, 1864
•*Tellina pacifica* Dall, 1900
•*Ventricolaria isocardia* (Verrill, 1870)

• Records from M. Montoya, P.O. Box 6327, San Jose, Costa Rica, pers. comm.
+ Indo-Pacific.

Isla de Malpelo

Isla de Malpelo (4°N) lies approximately 450 km west of Colombia (Fig. 24). It has a well-developed coral reef, and the subtidal zone consists of steeply sloping rocky walls (Birkeland et al. 1975). The bivalve fauna is virtually unknown, with only eight species listed (Birkeland et al. 1975), while a specimen of *Lyropecten subnodosus* (Sowerby, 1835) in the Los Angeles County Museum brings the total to nine (Table 16). No endemic or Indo-Pacific elements are present; the bivalve fauna is an integral part of the Panamic Province. Gorgona Island lies some 30 km off Ecuador and is not considered to be an oceanic island.

TABLE 16. Marine Bivalvia living at Isla de Malpelo.

Arca mutabilis (Sowerby, 1833)
Barbatia reeveana (Orbigny, 1846)
Hyotissa solida (Sowerby, 1871)
Isognomon quadratus (Anton, 1837)
Lithophaga aristata (Dillwyn, 1817)
Lithophaga plumula (Hanley, 1844)
Lyropecten subnodosus (Sowerby, 1835)
Septifer zeteki Hertlein & Strong, 1946
Striostrea prismatica (Gray, 1825)

Archipiélago de Colón

The Archipiélago de Colón (Galapagos Islands), situated approximately 1000 km west of Ecuador (Fig. 24), includes the most extensive group of oceanic islands in the eastern Pacific region. Pliocene (Dall and Ochsner 1928; Hertlein 1972) and Pleistocene (Hertlein and Strong 1939) deposits are represented, though some recent evidence suggests that the oldest strata are Pliocene or younger (Cox 1983). However, the age of terrestrial deposits is not highly significant to the consideration of neritic faunas, as it is probable that the insular shelf zone may have long existed as a submerged ridge projecting off the Nicoya Peninsula of Costa Rica and would have developed an offshore 'bank' fauna by the early Miocene, prior to the volcanism that raised the islands. The situation proposed is analagous to the presently rich fauna of Cortez Bank, some 120 km off southern California. There also exists evidence to suggest that the present group of islands represents the most westerly emergent remnants of an eastward extending volcanic chain (Holden and Dietz 1972) which could have provided a stepping-stone from the adjacent mainland. The similarity of fauna and flora to the mainland American area and particularly, the Caribbean, early suggested that the archipelago was at one time connected to that region (Baur 1891).

Much attention has been focused on the marine environment of this group of islands. Factors influencing marine biogeography were reviewed by Abbott (1966) and marine benthic zonation was studied by Cinelli and Colantoni (1974). Though systematic collecting occurred prior to 1829 (Howell 1941), the bivalve fauna remained poorly understood and erroneous concepts of extreme depauperation and endemicity prevail. The initial published inventory listed 16 bivalves (Carpenter 1857) and the last comprehensive catalogue based on systematic research cited 38 species (Hertlein and Strong 1955). Various publications added a few taxa (e.g. Schwengel 1938; Hertlein and Strong 1955) or confirmed previous records, but in general bivalves appeared sparingly (Smith 1877; Wimmer 1879; Stearns 1893). Even the most recent expedition mentions only nine species of bivalves (Taviani 1979). The standard text for the region (Keen 1971) with corrections and additions (Keen and Coan 1975) lists 44 species. Bernard (1983) consulted collections in European and American museums and the Allan Hancock Pacific Expeditions collection at the University of Southern California, and published a catalogue which identified 90 bivalve species from the Archipiélago de Colón. Finet (1985) issued a list of 91 bivalves based on identified museum collections and on Bernard (1983). The unworked Allan Hancock bivalve holdings were transferred to the Los Angeles County Museum of Natural History and underwent preliminary curation. In the spring of 1985, these bivalve lots were reviewed and 17 errors found in the identifications given by Bernard (1983) (Table 17). The opportunity was taken at this time to consult other materials in the Los Angeles County Museum taken by the *Anton Bruun* Expeditions, R/V *Searcher* 308 Cruise, *Ameripagos* 1, and the Los Angeles County Museum Expedition of May 1984. These collections yielded an aggregate 686 lots from 287 stations (Fig. 26) for a total of 186 species of bivalves (including 17 species on deposit at other institutions). These are listed in Table 18. Numerous minute bivalves from 52 Allan Hancock Foundation benthic mud samples remain to be worked up and will doubtless add several new records.

The bivalve fauna of this island group can no longer be considered depauperate in the sense of some of the Indo-Pacific insular faunas, and in particular, Hawaii. The number of bivalves is in line with that expected, judging by the distance to the mainland and prevailing oceanic currents. It does remain significantly attenuated

TABLE 17. Rejected records of Bivalvia from Archipiélago de Colón.

Anadara aequatorialis (Orbigny, 1846)
Brachidontes purpuratus (Lamarck, 1819)
Chione subrugosa (Wood, 1828)
Corbula biradiata Sowerby, 1833
Donax californicus Conrad, 1837
Donax gracilis Hanley, 1845
Gregariella chenuana (Orbigny, 1846)
Hyotissa hyotis (Linné, 1758)
Mactra velata Philippi, 1849
Mactrellona exoleta (Gray, 1837)
Megapitaria squalida (Sowerby, 1835)
Modiolus rectus (Conrad, 1837)
Noetia reversa (Sowerby, 1833)
Petricola amygdalina Sowerby, 1834
Protothaca asperrima (Sowerby, 1835)
Tivela byronensis (Gray, 1838)
Trachycardium procerum (Sowerby, 1833)

Isla del Coco

Isla del Coco, situated at 6°N (Fig. 24), some 500 km west of Costa Rica, carries some suggestion that it may have been part of a westward peninsula extending off Costa Rica during the Miocene (Vinton 1951). The molluscan fauna was, until recently, almost unknown (Biolley 1907, 1935; Hertlein 1932; Emerson 1967). Montoya (1983) included only 16 species of bivalves. Materials collected by the Allan Hancock Pacific Expeditions, now in the Los Angeles County Museum of Natural History, and by D.R. Shasky, presently in the Santa Barbara Museum, increase the fauna to 38 species. The efforts of Montoya and his associates (M. Montoya, P.O. Box 6327, San Jose, Costa Rica, pers. comm.) have expanded the known bivalve fauna to 80 species and we have included their additional records (Table 15). No endemic species are present and only seven are Indo-Pacific. Some 84% of the fauna is West American, and 70% of the bivalves are present on some of the other American oceanic islands. The record of Emerson (1978) of *Isognomon quandrangularis* (Reeve, 1858) is probably referable to *I. quadratus* (Anton, 1837), a common species of the West Pacific region. *Lopha folium* (Linne, 1758) is cosmopolitan in distribution, while both *Isognomon incisum* (Conrad, 1837) and *Cardita aviculina* Lamarck, 1819, are also Indo-Pacific. Isla del Coco is subject to an ocean current regime similar to that experienced by Île Clipperton, and in winter receives the eastward flow of the Equatorial Counter Current (Fig. 25). The relative proximity of the American continent, and the increased distance to be crossed by Indo-Pacific teleplanktonic larvae, may explain the poor representation of West Pacific elements compared to those of Île Clipperton. We consider Isla del Coco to be part of the Panamic Province.

TABLE 15. Living Marine Bivalvia occurring at Isla del Coco.

**Americardia guanacastensis* (Hertlein & Strong, 1947)
**Amerycina colpoica* (Dall, 1913)
Anadara grandis (Broderip & Sowerby, 1839)
Anadara multicostata (Sowerby, 1833)
Anadara rheinharti (Lowe, 1833)
Anomia peruviana Orbigny, 1846
Arca mutabilis (Sowerby, 1833)
**Arca pacifica* (Sowerby, 1833)
Arcopsis solida (Sowerby, 1833)
Argopecten circularis (Sowerby, 1835)
**Atrina tuberculosa* (Sowerby, 1835)
**Barbatia gradata* (Broderip & Sowerby, 1829)
**Barbatia reeveana* (Orbigny, 1846)
Cardita aviculina Lamarck, 1819+
Cardites laticistata (Sowerby, 1833)
**Chama squamuligera* Pilsbry & Lowe, 1932
**Codakia distinguenda* (Tryon, 1872)
**Condylocardia hippopus* (Mörch, 1861)
**Corbula esmeralda* Olsson, 1961
**Corbula porcella* Dall, 1916
Crenella divaricata (Orbigny, 1843)

TABLE 15. *(Continued)*

**Ctena clarionensis* Hertlein & Strong, 1946
Cyclopecten cocosensis (Dall, 1908)
Cyclopecten exquisitus Grau, 1959
**Cymatioa eletris* (Berry, 1963)
Diplodonta subquadrata Carpenter, 1856
**Divalinga eburnea* (Reeve, 1850)
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Gastrochaena rugulosa Sowerby, 1834
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Lima tetrica Gould, 1851
**Limatula similaris* (Dall, 1917)
Limopsis dalli (Lamy, 1912)
Lithophaga aristata (Dillwyn, 1817)
**Lithophaga calyculata* (Carpenter, 1857)
**Lithophaga plumula* (Hanley, 1844)
Lithophaga peruviana (Orbigny, 1846)
Lopha folium (Linné, 1758)+
Lyropecten subnodosus (Sowerby, 1835)
Malleus regulus (Forskål, 1775)+
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**Saccostrea palmula* (Carpenter, 1857)
**Semele formosa* (Sowerby, 1833)
**Semele purpurascens* (Gmelin, 1791)
Semele rupium (Sowerby, 1833)
Septifer zeteki Hertlein & Strong, 1946
**Solecardia eburnea* Conrad, 1849
Spondylus linguaefelis Sowerby, 1847
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Hyotissa hyotis (Linné, 1758)
Mactra velata Philippi, 1849
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Megapitaria squalida (Sowerby, 1835)
Modiolus rectus (Conrad, 1837)
Noetia reversa (Sowerby, 1833)
Petricola amygdalina Sowerby, 1834
Protothaca asperrima (Sowerby, 1835)
Tivela byronensis (Gray, 1838)
Trachycardium procerum (Sowerby, 1833)

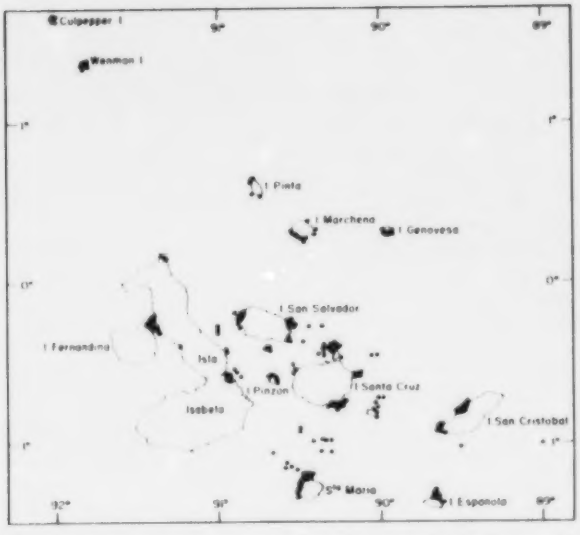

FIG. 26. Stations occupied by various expeditions to the Archipiélago de Colón that have yielded Bivalvia.

TABLE 18. Marine Bivalvia living in the Archipiélago de Colón (Galapagos Islands).

Acesta diomedia (Dall, 1908)+
Agerostrea megodon (Hanley, 1846)
Aligena cokeri Dall, 1909
Amerycina colpoica (Dall, 1913)
Anadara biangulata (Sowerby, 1833)
Anadara multicostata (Sowerby, 1833)
Anadara nux (Sowerby, 1833)
Anadara perlabiata (Grant & Gale, 1931)
Anomia peruviana Orbigny, 1846
Arca mutabilis (Sowerby, 1833)
Arca pacifica (Sowerby, 1833)
Arcopsis solida (Sowerby, 1833)
Argopecten circularis (Sowerby, 1835)
Atrina texta Hertlein, Hanna & Strong, 1943
Atrina tuberculosa (Sowerby, 1833)
Bankia cf. *gouldi* (Bartsch, 1908)
Barbatia alternata (Sowerby, 1833)
Barbatia gradata (Broderip & Sowerby, 1829)
Barbatia lurida (Sowerby, 1833)
Barbatia reeviana (Orbigny, 1846)
Barbatia rostae Berry, 1954
Basterotia hertleini Durham, 1950
Basterotia peninsularis (Jordan, 1936)
Brachidontes adamsianus (Dunker, 1853)
Brachidontes puntarensis (Pilsbry & Lowe, 1932)
Cardiomya balboae (Dall, 1916)
Cardiomya californica (Dall, 1886)
Cardiomya costata (Sowerby, 1834)
Cardiomya lanieri (Strong & Hertlain, 1937)
Cardita affinis Sowerby, 1833
Cardites crassicostata (Sowerby, 1825)
Cardites grayi (Dall, 1903)
Cardites laticostata (Sowerby, 1837)
Chama buddiana C.B. Adams, 1852
Chama echinata Broderip, 1833
Chama mexicana Carpenter, 1857°
Chama squamuligera Pilsbry & Lowe, 1932
Chione compta (Broderip, 1835)

TABLE 18. *(Continued)*

Chione crenifera Sowerby, 1835
Chione guatulcoensis Hertlein & Strong, 1940
Chione mariae (Orbigny, 1846)
Chione undatella (Sowerby, 1835)
Chlamys incatata Hertlein, 1972
Chlamys lowei (Hertlein, 1935)
Codakia punctata (Linné, 1758)
Condylocardia digueti Lamy, 1916
Condylocardia n.sp.
Corbula bicarinata Sowerby, 1833
Crassostrea columbiensis (Hanley, 1846)
Crassostrea palmula (Carpenter, 1858)
Crassinella pacifica C.B. Adams, 1852
Crassinella varians (Carpenter, 1857)
Crenella divaricata (Orbigny, 1847)
Ctena galapagana (Dall, 1901)
Ctena mexicana (Dall, 1901)
Cumingia lamellosa Sowerby, 1833
Cyathodonta galapagana Dall, 1915
Cyclinella subquadrata (Hanley, 1845)
Cyclocardia beebei (Hertlein, 1958)
Cyclopecten cf. *barbarensis* Grau, 1959
Cyclopecten exquisitus Grau, 1959
Cyclopecten lioope (Dall, 1908)
Cyclopecten pernomus (Hertlein, 1935)
Cyclopecten polyleptus (Dall, 1908)
Cyclopecten cf. *vitreus* (Gremlin, 1791)
Cyclopecten zacae (Hertlein, 1935)
Cymatioa electilis (Berry, 1963)
Cymatioca undulata (Hanley, 1844)
Dacrydium elegantulum Soot-Ryen, 1955
Dacrydium panamensis Knudsen, 1970
Diplodonta subquadrata Carpenter, 1856
Divalinga eburnea (Reeve, 1850)
Dosinia dunkeri (Philippi, 1844)
Dosinia ponderosa (Schumacher, 1817)
Eucrassatella gibbosa (Sowerby, 1832)
Fugleria illota (Sowerby, 1833)°
Galeomella peruviana (Olsson, 1961)
Gari helenae Olsson, 1961
Gastrochaena ovata Sowerby, 1834
Gastrochaena rugulosa Sowerby, 1834
Gouldia california Dall, 1917
Glycymeris inaequalis (Sowerby, 1833)
Glycymeris lintea Olsson, 1961
Glycymeris maculata (Broderip, 1832)
Glycymeris multicostata (Sowerby, 1833)
Gregariella caenui (Récluz, 1842)
Gregariella coralliophaga (Gmelin, 1791)
Halicardia perplicata (Dall, 1890)
Haliris aequacostata (Howard, 1950)
Halodakra subtrigona (Carpenter, 1857)
Hiatella solida (Sowerby, 1834)
Hyalopecten neoceanus (Dall, 1908)+
Hyotissa solida (Sowerby, 1871)
Isognomon janus Carpenter, 1857
Isognomon quadratus (Anton, 1837)
Laevicardium elenense (Sowerby, 1841)
Lasaea petitiana (Récluz, 1843)
Leporimetis cognata (Pilsbry & Vanata, 1902)
Lima tetrica Gould, 1851
Limopsis cf. *dalli* Lamy, 1912
Limopsis zonalis Dall, 1908
Lithophaga aristata (Dillwyn, 1817)
Lithophaga calyculata (Carpenter, 1857)°
Lithophaga laevigata (Quoy & Gaimard, 1835)

TABLE 18. *(Continued)*

Lithophaga plumula (Hanley, 1844)
Lopha frons (Linné, 1758)
Lucina cancellaris Philippi, 1846
Lucina centrifuga (Dall, 1901)
Lucina leucocymoides (Lowe, 1935)
Lyonsia californica Conrad, 1837
Leptopecten velero (Hertlein, 1935)
Lunarca brevifrons (Sowerby, 1833)
**Lyropecten magnificus* (Sowerby, 1835)
Lyropecten subnodosus (Sowerby, 1835)
Macoma grandis (Hanley, 1844)
Malleus regulus (Forskål, 1775)
Martesia cuneiformis (Sowerby, 1822)
Megapitaria aurantiaca (Sowerby, 1831)
Modiolus capax (Conrad, 1837)
Mytella strigata (Hanley, 1843)°
Neaeromya stearnsii (Dall, 1899)
Nemocardium pazianum (Dall, 1916)
Nucula exigua Sowerby, 1833
Nucula costellata (Sowerby, 1833)
Nuculana elenensis (Sowerby, 1833)
Nuculana hindsii (Hanley, 1860)
Nuculana ornata (Orbigny, 1845)
Nuculana polita (Sowerby 1833)
Nuculana pontonia (Dall, 1890)
Papyridea aspersa (Sowerby, 1833)
Parapholas calva (Sowerby, 1834)
**Pecten galapagensis* Grau, 1959
Pecten sericeus Hanley, 1845
Petricola concinna Sworby, 1834
Periglypta multicostata (Sowerby, 1835)
Phlyctiderma caelata (Reeve, 1850)°
Pinctada mazatlanica (Hanley, 1856)
Pitar catharius (Dall, 1902)
Pitar consanguineus (C.B. Adams, 1852)°
Pitar helenae Olsson, 1961
Pitar hoffstetteri Fischer-Piette, 1964†
Pitar perfragilis Pilsbry & Lowe, 1932
Placunanomia cumingi Broderip, 1832
Plectodon scaber Carpenter, 1864
Plicatula penicillata Carpenter, 1864
Plicatula spondylopsis Rochebrunne, 1895
Promantellum orbigny Lamy, 1930
Promantellum pacifica (Orbigny, 1846)
Protothaca grata (Sowerby, 1831)
Protothaca pertincta (Dall, 1902)
Protothaca zorritensis (Olsson, 1961)
Psammotreta aurora (Hanley, 1844)
Pseudochama clarionensis Willett, 1938
Pseudochama corrugata (Broderip, 1835)
Pseudochama janus (Reeve, 1847)
Pseudochama panamensis (Reeve, 1847)
Pseudochama saavedrai Hertlein & Strong, 1946
Pteria sterna (Gould, 1851)
Semele purpurascens (Gmelin, 1791)
Semele rupium (Sowerby, 1833)
Semele sowerbyi Tryon, 1869
Semele venusta (Reeve, 1853)
Semele n.sp.
Septifer zeteki Hertlein & Strong, 1946
Solecurtus lineatus (Gabb, 1861)
Sphenia luticola (Valenciennes, 1846)
Spondylus princeps Broderip, 1833
Strigilla chroma Salisbury, 1934
Strigilla serrata Mörch, 1860
Striostrea prismatica (Gray, 1825)

TABLE 18. *(Continued)*

Strophocardia megastropha (Gray, 1825)
Tagelus affinis (C.B. Adams, 1852)
**Transennella galapagana* Hertlein & Strong, 1939
Transennella modesta (Sowerby, 1835)
Transennella omissa (Pilsbry & Lowe, 1932)
Tellina amianta Dall, 1900
Tellina chrysocoma Dall, 1908
Tellina eburnea Hanley, 1844
Tellina cf. *hertleini* (Olsson, 1961)
Tellina mantaensis Pilsbry & Olsson, 1943
Tellina ochracea Carpenter, 1864
Tellina pacifica Dall, 1900
Tellina reclusa Dall, 1900
Trachycardium consors (Sowerby, 1833)°
Trigoniocardia granifera (Broderip & Sowerby, 1829)
Ventricolaria isocardia (Verrill, 1870)
Verticordia ornata (Orbigny, 1853)
Yoldiella sp. *indent.*

° California Academy of Sciences, San Francisco.
+ United States National Museum, Washington.
† Musée d'histoire naturelle, Paris.
* Endemic species.
Others in Los Angeles County Museum of Natural History.

compared to the 600 bivalve species occurring on the adjacent mainland coast (Bernard 1983). Less than 3% of the bivalves are endemic, a total in agreement with the early recognized low endemicity (Stearns 1893; Dall 1909) and follows the general case that evolutionary rates of marine invertebrates are lower than that of the terrestrial biota (James 1984). However, the situation is different in other groups. Brusca (1987) reported that 51% of the isopods are endemic. Only 2% of the bivalve fauna is Indo-Pacific in origin and 95% is Panamic. Warmwater Peruvian elements are present, but there are no Chilean species. Because of the strong clustering of sample sites, no inter-island zoogeographical differences can be detected, and the northernmost group (Islas Culpepper and Wenman) yields a similar group of species that merely appears to reflect substrate type. No evidence is present to support the idea that the deep water associated with these islands contains an endemic fauna. Hertlein and Strong (1939) remark on the Caribbean affinity of the molluscan fauna and 28% of the bivalves are Caribbean cognate species, somewhat higher than the mainland coast (20%). This suggests that the Archipiélago de Colón may have served as a refugium after the closure of the Isthmus of Panama. The terrestrial flora also displays a strong connection with the Caribbean (Svenson 1946), as does the avian fauna (Croizat 1958).

Isla San Felix

Isla San Felix and Isla San Ambrosio (26°S) lie approximately 600 km west of Chile (Fig. 24). They are small islets with precipitous shores. Structurally, these islands are the easternmost representatives of a series of seamounts stretching west to Islas de Pascua and Sala y Gomez of the Indo-Pacific region. However, the recent volcanic origin of both San Felix and San Ambrosio

suggests they were formed near their present site and do not represent eastward migrants on the Nazca Plate subducting under South America. This view is strengthened by the lack of an Indo-Pacific faunal element. The bivalve fauna is unknown except for four stations occupied by the *Anton Bruun* Cruise 17 in 1966 and on deposit in the Los Angeles County Museum of Natural History. These yielded 14 lots and 13 species of bivalves (Table 19), including two new species. This fauna includes no endemic species and 95% belong to the northern Chilean Province, though the two Panpacific species, *Lasaea petitiana* (Recluz, 1843) and *Hiatella solida* (Sowerby, 1834), are represented.

TABLE 19. Marine Bivalvia living at Isla San Felix.

Acesta diomedia (Dall, 1908)
Arca fernandezensis Hertlein & Strong, 1943
Argopecten purpuratus (Lamarck, 1819)
Barbatia pusilla (Sowerby, 1833)
Entodesma cuneatum (Gray, 1828)
Gregariella chenui (Récluz, 1842)
Hiatella solida (Sowerby, 1834)
Lasaea petitiana (Récluz, 1843)
Lima n.sp.
Limaria n.sp.
Limatula cf. *pygmaea* (Philippi, 1845)
Modiolus aurum Osorio, 1979
Propeamussium cf. *malpelonium* (Dall, 1908)

Islas Juan Fernandez

Islas Juan Fernandez (Fig. 24), comprising Isla Mas a Tierra, Isla Santa Clara and Isla Mas Afuera, lie some 600 km west of Valparaiso, Chile. They are the southernmost ocean islands of the eastern Pacific region. The bivalve fauna is virtually unknown, and limited to the five species cited by Stempell (1902), the summary by Dall (1909), the work by Odhner (1928) and the species listed by Rozbaczylo and Castilla (1987). Our information has been increased by the 12 stations occupied by the *Anton Bruun* Cruise 17 in 1966 on deposit in the Los Angeles County Museum of Natural History. This comprises 71 lots of 31 species, including three new to science, as well as material in the Museum of Comparative Zoology at Harvard University (Table 20). Some 68% of the bivalve fauna belongs to the Chilean (= Peruvian AUCTT.) Province, and no Indo-Pacific elements are present; 26% are endemic. This is the highest bivalve endemicity recorded for the oceanic islands of the Eastern Pacific Ocean. The frigid northward flowing Peru Current may isolate these islands from the mainland and prevent colonization and encourage endemicity. Three species also occur in the Archipiélago de Colón; of particular interest are living representatives of *Ervilia galapagana* Dall, 1928, and *Pholadomya cf. darwinii* Dall & Ochsner, 1928, species known only from fossils in the Archipiélago de Colón. The latter is also the first record of living *Pholadomya* in the eastern Pacific Ocean. Three species *Arca fernandezensis* Hertlein & Strong, 1943, *Gregariella chenui* (Récluz, 1846), and *Modiolus aurum* Osorio, 1979, are shared with Isla San Felix. The bivalve fauna is clearly assignable to the Chilean Province, but the high level of endemicity and the presence of living representatives known as fossils elsewhere would make further exploration rewarding. It is possible that the apparent high endemicity is merely a result of poor knowledge of the fauna of the adjacent mainland coasts of South America. *Ervilia* and *Irusella* and possibly *Lasaea* are of Tethyan origin and may represent a remnant of a previously widespread transisthmian fauna. This supposition is strengthened by the discovery of living *Pholadomya* related or identical with the fossil *P. darwini* Dall & Ochsner, 1928, from the Archipiélago de Colón and probably referable to *P. candida* Sowerby, 1823, a rare inhabitant of the Caribbean region. *Melliteryx,* on the other hand, is a living genus from New Zealand, Australia, and north to Japan.

TABLE 20. Marine Bivalvia living at Islas Juan Fernandez.

**Amygdalum americanum* Soot-Ryen, 1955
Arca fernandezensis Hertlein & Strong, 1943
Bankia martensi (Stempell, 1899)
Barbatia magellanica (Gmelin, 1791) +
Chama pellucida Broderip, 1835
Chlamys phalara Roth, 1975
Condylocardia n.sp.
Cuspidaria chilensis Dall, 1908
Cuspidaria cf. *patagonica* (E.A. Smith, 1885)
Cuspidaria n.sp.
Erycina platei (Stempell, 1899) +
**Ervilia galapagana* Dall, 1928
**Ervilia producta* Odhner, 1922
Gari solida (Gray, 1828)
Gregariella chenui (Récluz, 1842)
**Irusella fernandiziana* Stempell, 1899
Kellia tumbesiana Stempell, 1899
**Lasaea macrodon* Stempell, 1899
**Melliteryx* ? n.sp.
Modiolus aurum Osorio, 1979
Mytella speciosa (Reeve, 1857)
**Nucula fernandensis* Villarroel, 1971
Nucula grayi Orbigny, 1846
Nucula pisum Sowerby, 1833
Pandora cistula Gould, 1850
Philobrya antarctica (Philippi, 1868)
Philobrya brattstroemi Soot-Ryen, 1957
**Pholadomya* cf. *darwini* Dall & Ochsner, 1928
Promantellum orbignyi Lamy, 1930
Pseudochama janus (Reeve, 1847)
Xylophala globosa Sowerby, 1835 +

* Endemic species.
+ From Rozbaczylo and Castilla (1987).

The Insular Faunas

The distribution and nature of these insular bivalve faunas is summarized in Table 21. Comparative analysis of the bivalve fauna of the eastern Pacific oceanic islands is probably premature as only the Archipiélago de Colón has received adequate exploratory coverage. A meaningful comparison presumes that the majority of the fauna is known, or at least, all the islands have received

TABLE 21. Relative percentage by origin of the total marine Bivalvia of the eastern Pacific Oceanic Islands, Hawaii, and Isla de Pascua. *N* = number of species.

Locality	*N*	Endemic	West America	Indo-Pacific
Isla de Guadalupe	20	0	100	0
Islas de Revillagigedo	28	0	100	0
Île Clipperton	20	5	85	10
Isla del Coco	80	0	96	4
Isla De Malpelo	9	0	100	0
Archipiélago de Colón	186	3	95	2
Isla San Felix	13	0	85	15
Islas Juan Fernandez	28	26	74	0
Hawaii	150	37	2	61
Isla de Pascua	15	13	13	74

equal collecting effort. This is not the case and the dramatic increase in the bivalve fauna known from the Archipiélago de Colón reported herein emphasizes the requirement for more exploration. Acknowledging this bias, there nevertheless remains a significant correlation between area of the neritic zone and number of bivalve species present. All the eastern Pacific oceanic islands show a strong or exclusive West American component, with only weak influence from the Indo-Pacific areas overwhelmingly present in the Hawaiian Archipelago and Isla de Pascua.

Ordination of the insular faunas using a principal coordinates analysis shows the distance between islands as a function of faunal similarity (Fig. 27), derived from a similarity matrix of the incidence data. It reveals a vertical ordering generally following their latitudinal positions, strongly reinforcing the hypothesis of an arc of insular faunas reaching from the Islas de Revillagigedos to the Archipiélago de Colón (Croizat 1958). The horizontal axis separates the Indo-Pacific and West American components.

The bivalve fauna of Isla de Guadalupe and the Islas de Revillagigedo are exclusively West American, but they share only two species, as the northern island is a faunal outrider of the California Province whereas the southern group is Panamic. The numerous bivalve species shared by the Archipiélago de Colón and the mainland Panamic Province carries it close to America, while the small Indo-Pacific element on Clipperton, Coco, and San Felix distance them from America.

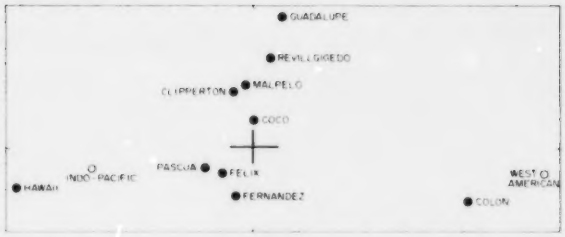

FIG. 27. Principal coordinates analysis of the living marine Bivalvia of the eastern Pacific Oceanic Islands, Hawaii and Isla de Pascua (calculated using the step-across analysis of Williamson 1978).

Endemic bivalve species are numerous in Hawaii and to a lesser extent, Isla de Pascua. In the eastern Pacific Ocean Islands, they are remarkably absent except in the South American Islas Juan Fernandez. It appears that there is not a strong barrier between the West American coast and the Oceanic Islands, but the vigorous northwards flowing Peru Current may help to isolate Islas Juan Fernandez. Offshore gyres of the Peru Current, impinging on Islas San Felix and San Ambrosio and more distantly, on Isla de Pascua, may account for their West American components (Fig. 28). A diagram of provinciality of the eastern Pacific Ocean, including the offshore islands, is shown in Fig. 29.

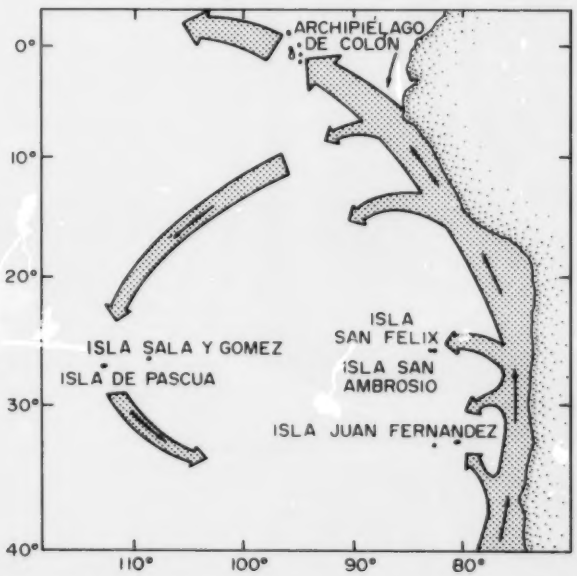

FIG. 28. Surface currents associated with the Peru Current, showing possible connections between Isla de Pascua, Archipiélago de Colón, and Islas Juan Fernandez.

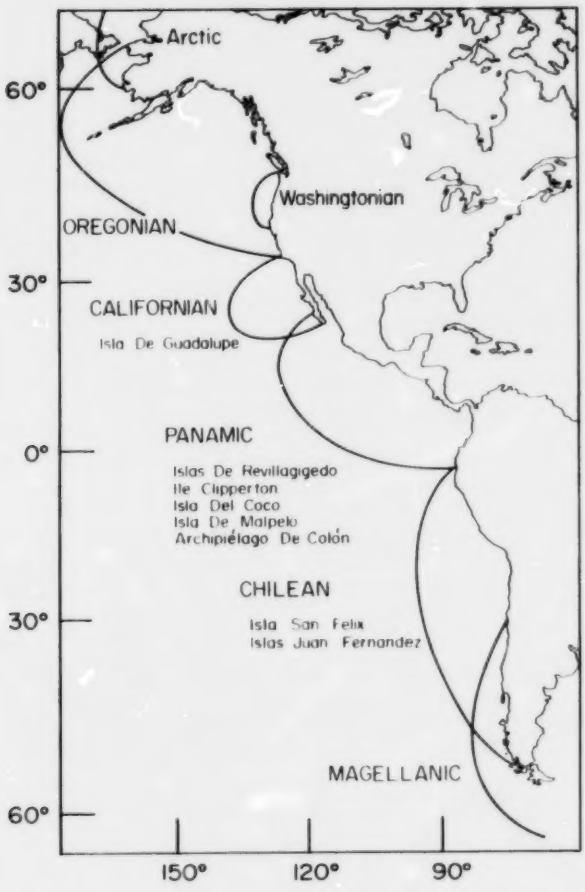

FIG. 29. Summary of bivalve provinces and subprovinces of the eastern Pacific Ocean, including offshore islands.

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NOTE:

Dr. Frank Bernard died before he could make final revisions to his manuscript, and so I assumed responsibility for them. I have tried to revise the manuscript as I felt Frank would have done.

GLEN JAMIESON

References

ABBOTT, D. P. 1966. Factors influencing the zoogeographic affinities of the Galapagos inshore marine fauna, p. 108–122. *In* R. I. Bowman [ed.] The Galapagos. Proc. Symp. Galapagos Int. Sci. Proj. Univ. Calif. Press, Berkeley, CA. 318 p.

ADDICOTT, W. O. 1966. New Tertiary marine mollusca from Oregon and Washington. J. Paleont. 40: 635–646.

1969. Late Pliocene molluscs from San Francisco Peninsula, California, and their paleogeographic significance. Proc. Calif. Acad. Sci. 37: 57–93.

1970. Latitudinal gradients in Tertiary molluscan faunas of the Pacific coast. Palaeogeogr. Palaeoclimatol. Palaeocol. 8: 287–312.

1977. Neogene chronostratigraphy of nearshore marine basins of the Eastern North Pacific. Proc. 1st Int. Congr. Pacific Neogene. Tokyo. 1976: 151–175.

ADDICOTT, W. O., R. Z. POORE, J. A. BARRON, H. D. GOWER, AND K. MCDOUGALL. 1978. Neogene biostratigraphy of the Indian Creek and Shell Creek area. Northern La Panza Range, California. U.S. Geol. Surv. Rep. 78/466: 49–81.

ALLAN, R. S. 1963. On the evidence of Austral Tertiary and Recent Brachiopods on Antarctic biogeography, p. 451–454. *In* J. L. Gressitt [ed.] Pacific Basin Biogeography. 10th Pac. Sci. Congr. Honolulu, Hawaii. 1961: 561 p.

ALLEN, C. R. 1957. San Andreas Fault zone in San Gorgonia Pass, Southern California. Bull. Geol. Soc. Am. 68: 315–350.

ALLISON, R. C. 1978. Late Oligocene through Meistocene molluscan faunas in the Gulf of Alaska region. Veliger 21(2): 171–188.

ALLISON, R. C., AND L. MARINCOVICH. 1981. A Late Oligocene or earliest molluscan fauna from Sitkinak Island, Alaska. U.S. Geol. Surv. Prof. Pap. 1233: 11 p., 3 pls.

ANDREWS, J. A. 1985. True polar wander: an analysis of Cenozoic and Mesozoic paleomagnetic poles. J. Geophys. Res. 90: 7737–7750.

ARMENTROUT, J. M., R. J. ECHOLS, AND K. W. NASH. 1978. Late Neogene climatic cycles of the Yakataga Formation, Robinson Mountains, Gulf of Alaska area. Stanford Univ. Pub. Geol. Sci. 14: 3–4.

AUER, V. 1960. The Quaternary history of Fuegan Patagonia, p. 507–516. *In* C. F. A. Pantin [ed.] A discussion on the biology of the southern cold temperate zone. Proc. Roy. Soc. London 152B: 429–677.

1966. Climatic variations in Fuego Patagonia, p. 37–55. *In* D. I. Blumenstock [ed.] Pleistocene and Post-Pleistocene climatic variations in the Pacific area. Honolulu. Bishop Mus. Press. 182 p.

AXELROD, D. I., AND H. P. BAILEY. 1969. Paleotemperature analysis of Tertiary floras. Palaegeogr. Palaeoclimatol. Palaeocol. 6: 163–195.

BALECH, E. 1954. Division zoogeografica del litoral sudamericana. Rev. Biol. Mar. 4: 184–195.

BALL, I. R. 1976. Nature and formulation of biogeographical hypotheses. Syst. Zool. 24: 407–430.

BANDY, O. O. 1964. Planktonic foraminiferal criteria for paleoclimate zonation. Sci. Rep. Tohoku Univ. (Ser. 2) Geol. Spec. Vol. 4: 1–8.

BARTSCH, P. 1912. A zoogeographic study based on the pyramidellid mollusks of the west coast of America. Proc. U.S. Nat. Mus. 42: 297–349.

1921. Ocean currents, the prime factor in the distribution of marine mollusks on the west coast of America. Bernice P. Bishop Mus. Spec. Publ. 7: 505–526.

BARTSCH, P. AND H. REHDER. 1939. Mollusks collected on the Presidential cruise of 1938. Smithsonian Misc. Coll. 98: 1-18.

BAUR, G. 1891. On the origin of the Galapagos Islands. Am. Nat. 25: 217-229, 307-326.

BEKLEMISHEV, K. V. 1982. O prirodie biogeograficheskikh dokazatel'stv. [On the nature of biogeographical evidence], p. 5-11. *In* O. G. Kassakin and A. I. Kafanov [ed.] Morskaya biogeografiya: predmet, metody, printsipy rayonirovniya. [Marine biogeography: subject matter, methods, principles of zoning.] NAUKA Moscow. 311 p. (Can. Transl. Fish. Aquat. Sci. 5054, 1984).

BERG, L. S. 1918. O prichinakh skhodstva fauna severnykh chastey Atlanticheskogo i Takhogo okeanov [On the causes of the resemblance in the faunas of the Northern part of the Atlantic and Pacific Oceans]. Bull. Sov. Acal. Sci. 3: 92-97.

1933. Die bipolare Verbreitung der Organismen und die Eiszeit. Zoogeographica 1: 444-484.

BERGSTROM, S. M. 1973. Ordovician conodonts, p. 47-58. *In* A. Hallam [ed.] Atlas of Palaeobiogeography. Elsevier, Amsterdam.

BERNARD, F. R. 1979. Bivalve mollusks of the western Beaufort Sea. Contrib. Sci. Nat. Hist. Mus. Los Angeles. 313: 80 p.

1983. Catalogue of the living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. Can. Spec. Publ. Fish. Aquat. Sci. 61: 102 p.

BIOLLEY, P. 1907. Mollusques de L'Isla Del Coco. Mus. Nat. Costa Rica for 1907. 1-30. [Also appeared 1908. An. Mus. San Salvador 3: 327-333].

1935. Moluscos de la Isla Del Coco. (Resultados de una expedicion hectio en Enera de 1903, del 11 21 16, banjo los auspicios del gobienra de Costa Rica). Rev. Colegia Superior de Senoritas 2: 1-24.

BIRKELAND, C., D. L. MEYER, J. P. STAMES, AND C. L. BUFORD. 1975. Subtidal communities of Malpelo Island, p. 55-68. *In* J. B. Graham [ed.] The biological investigation of Malpelo Island, Colombia. Smithsonian Contrib. Zool. 176: 98 p.

BOUCOT, A. J. 1975. Standing diversity of fossil groups in successive intervals of geologic time viewed in the light of changing levels of provincialism. J. Paleontol. 49: 1105-1111.

BOUCOT, A. J., J. G. JOHNSON, AND J. A. TALENT. 1969. Early Devonian Brachiopod zoogeography. Geol. Soc. Am. Spec. Pap. 119: 113 p.

BRATSTROM, H., AND A. JOHNSSEN. 1983. Ecological and regional zoogeography of the marine benthic fauna of Chile. Sarsia 68: 289-339.

BRETSKY, P. W. 1973. Evolutionary patterns in the Paleozoic Bivalvia: Documentation and some theoretical considerations. Bull. Geol. Soc. Am. 84: 2079-2096.

BRIGGS, J. C. 1974. Marine zoogeography. McGraw-Hill, New York, NY. 476 p.

BRUSCA, R. C. 1987. Biogeographic relationships of Galapagos marine isopod crustaceans. Bull. Mar. Sci. 41: 268-281.

BRUSCA, R. C., AND D. A. THOMSON. 1975. Pulmo Reef: the only 'coral reef' in the Gulf of California. Cienc. Mar. Univ. Autonoma de Baja California, 21: 37-53.

BRUSCA, R. C., AND B. R. WALLERSTEIN. 1979. Zoogeographic patterns on idoteid isopods in the northeast Pacific, with a review of shallow water zoogeography of the area. Bull. Biol. Soc. Washington. 3: 67-105.

BUONANNI, F. 1681. Ricreatione dell'occhio a della mente nell' osservation' delle Chiocciole, proposta a' curiosi delle opere della natura, &. Roma, 4 parts, pp. xiv, 384, 109 pls., 3 engraved title-pages, e engraved half-titles, 4 to.

CAMPBELL, C. A., AND J. W. VALENTINE. 1977. Comparison of modern and ancient marine provinces. Paleobiology 3: 49-57.

CARCELLES, A. R. 1950. Catalogo de los Moluscos Marinos de la Patagonia. Mus. Nahuel Huapi Perito. Anales 2: 41-100.

CARPENTER, P. P. 1857. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Rep. Brit. Assoc. Adv. Sci. (for 1856): 159-368, pls. 6-9.

CASTILLA, J. C., AND N. ROZBACZYLO. 1987. Invertebrados marinos de Isla de Pascua y Sala y Gomez. Islas Oceanicas Chileans: 191-215.

CHACE, E. P. 1958. The marine molluscan fauna of Guadalupe Island, Mexico. Trans. San Diego Soc. Nat. Hist. 12: 319-332.

CHURKIN, M., AND J. H. TREXLER. 1981. Continental plates and accreted oceanic terranes in the Arctic, p. 1-20. *In* A. E. M. Nairn, M. Churkin, and F. G. Stehli [ed.] The ocean basins and margins. Vol. 5. The Arctic Ocean. Plenum Press, New York, NY.

CINELLI, F., AND P. COLANTONI. 1974. Alcune observazioni sulla zonazione del benthos marino sulle coste rocciose delle Isole Galapagos (Oceano Pacifico). Mus. Zool. Univ. Firenze. 22 p. 17 figs.

CLARKE, A. H. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. Nat. Mus. Canada Bull. 181: 114 p.

CONNELL, J. H., AND E. ORIAS. 1964. The ecological regulation of species diversity. Am. Nat. 98: 399-414.

CONNOR, E. F., AND E. D. MCCOY. 1979. The statistics and biology of the species are relationship. Am. Nat. 113: 791-833.

COX, A. 1983. Age of the Galapagos Islands, p. 11-23. *In* R. I. Bowman, M. Berson, and A. E. Leviton [ed.] Patterns of evolution in Galapagos organisms. Am. Assoc. Adv. Sci. San Francisco, CA.

CRADDOCK, C., AND C. D. HOLLISTER. 1976. Geologic evolution of the southwest Pacific Basin, p. 723-744. *In* Initial reports. Deep-Sea drilling project. Washington, DC. 35.

CRAME, J. A. 1983. The occurrence of the Upper Jurassic bivalve *Malayomaorica malayomaorica* (Krumbeck) on the Orville Coast, Antarctica. J. Molluscan Stud. 49: 61-76.

CRAMER, F. M. 1971. Indications from Middle Paleozoic palynofacies transgressions for the rate of crustal movement, especially during the Wenlochian. An. Acad. Bras. Cienc. 43 (Suppl.): 51-66.

CROIZAT, L. 1958. Panbiogeography or an introductory synthesis of zoogeography, phytogeography, and geology: with notes on evolution, systematics, ecology, anthropology, etc. Wheldon and Wesley, England. 3 vols.

CROIZAT, L., G. NELSON, AND D. E. ROSEN. 1974. Center of origin and related concepts. Syst. Zool. 23: 265-287.

DAHL, E. 1960. The cold temperate zone in Chilean seas. Proc. Roy. Soc. London 152 (B): 631-633.

DALL, W. H. 1893. A subtropical Miocene fauna in Arctic Siberia. Proc. U.S. Nat. Mus. 16: 471-478.

1895. New species of shells from the Galapagos Islands. Nautilus 8: 126-127.

1908. Report on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer 'Albatross' during 1899, Lieut. Commander Z. L. Tanner U.S.N., commanding. No. 37. Reports on the scientific results of the expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz by the U.S.

Fish Commission steamer 'Albatross' from October, 1904, to March, 1905. Lieut. Commander L. M. Garrett, U.S.N., commanding. No 14. The Mollusca and Brachipoda. Bull. Mus. Comp. Zool. Harvard 43: 205:487, 22 pls.

1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proc. U.S. Nat. Mus. 367: 147-294, pls. 20-28.

1916. On some anomalies in geographic distribution of Pacific coast Mollusca. Proc. Nat. Acad. Sci. 2: 700-703.

1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species. U.S. Nat. Mus. Bull. 112: 217 p., 22 pls.

DALL, W. H., P. BARTSCH, AND H. A. REHDER. 1938. A manual of the Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. Bernice P. Bishop Mus. Bull. 153: 233 p., 57 pls.

DALL, W. H., AND W. H. OCHSNER. 1928. Tertiary and Pleistocene mollusks from the Galapagos Islands. Proc. Calif. Acad. Sci. (Ser. 4) 17: 89-139, pls 2-7.

DARWIN, C. 1859. On the origin of species. J. Murray. London.

DAUTZENBERG, P. 1896. Liste de mollusques du Chile. Actes Soc. Sci. Chili. 6: 64-67.

DAWSON, E. X. 1951. A further study of upwelling and associated vegetation along Pacific Baja California, Mexico. J. Mar. Res. 10: 34-58.

DELL, R. K. 1964. Antarctic and Subantarctic Mollusca: Amphineura, Scaphopoda, and Bivalvia. Discovery Rep. 33: 93-250.

DERJUGIN, K. 1927. La distribution bipolaire des organismes marins. Bull. Inst. Oceanogr. Mar. 49: 1-23.

DEVEREUX, I. 1967. Oxygen isotope paleotemperature measurements on New Zealand Tertiary fossils. N.Z. J. Sci. 10: 988-1011.

DICKINSON, J. J., AND A. G. CAREY. 1978. Distribution of gammarid amphipoda (Crustacea) in Cascadia Abyssal Plain (Oregon). Deep-Sea Res. 25: 97-106.

DIETZ, R. S., AND J. C. HOLDEN. 1970. Reconstruction of Pangaea: breakup and dispersion of continents, Permian to present. J. Geophys. Res. 75: 4939-4956.

DOBZHANSKY, T. 1950. Evolution in the tropics. Am. Sci. 38: 209-221.

DODIMEAD, A. J., AND H. J. HOLLISTER. 1958. Progress report of drift bottle releases in the northwest Pacific Ocean. J. Fish. Res. Board Can. 15: 851-865.

DOUGLAS, R. G., AND S. M. SAVIN. 1971. Oxygen and carbon isotope analyses of Cretaceous and Tertiary Foraminifera in the central North Pacific. In. Reps. DSDP 17: 591-606.

DOW, R. L. 1973. Fluctuations in marine species abundance during climatic cycles. MTS J. 7: 38042.

DURHAM, J. W., AND E. C. ALLISON. 1960. The geologic history of Baja California and its marine faunas. Syst. Zool. 9: 47-91.

EKMAN, S. 1935, 1953. Zoogeography of the sea. Sidgwick and Jackson, London. 417 p.

ELDHOLME, I., AND J. THIEDE. 1980. Cenzoic continental separation between Europe and Greenland. Palaeogeogr. Palaeoclimatal. Palaeoecol. 30: 243-259.

EMERSON, W. K. 1956. Upwelling and associated marine life along Pacific Baja California, Mexico. J. Paleontol. 30: 393-397.

1967. Indo-Pacific faunal elements in the tropical Eastern Pacific, with special reference to the mollusks. Jpn. J. Malacol. 25: 85-93.

1978. Mollusks with Indo-Pacific faunal affinities in the Eastern Pacific Ocean. Nautilus 92: 91-96.

FAIRBRIDGE, R. W. 1973. Glaciation and plate migration, p. 17-24. *In* D. H. Tarling, and S. K. Runcorn [ed.] Implications of continental drift to the earth sciences. Academic Press, New York, NY.

FARQUHAR, H. 1908. The bipolar theory. Trans. Proc. New Zealand Inst. 40: 259-261.

FINET, Y. 1985. Preliminary faunal list of the marine mollusks of the Galapagos Islands. Inst. Roy. Sci. Nat. Belgique Doc. de travail 20: 50 p.

FINN, R. 1986. Travels of a Terrane. Engineering & Science 49: 32-33.

FISHER, A. G. 1960. Latitudinal variations in organic diversity. Evolution 14: 64-81.

FISCHER, P. 1858. Note sur la distribution géographique de quelques mollusques. J. Conchyliol 7: 119-122.

1880-1887. Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossiles. Paris. XXIV + 1369 p., 24 pls.

FLESSA, K. W., AND J. J. SEPKOSKI. 1978. On the relationship between Phanerozoic diversity and changes in habitable area. Paleobiology 4: 359-366.

FLINT, R. 1957. Glacial and Pleistocene geology. Wiley, New York. 272 p.

FORBES, E. 1844. Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as bearing on geology. Brit. Assoc. Adv. Sci. (for 1843): 130-193.

FUENTES, F. 1914. Contribucion al estudio de la fauna de la Isla de Pascua. Bol. Mus. Nac. Chile 7: 285-317.

GARTH, J. S. 1957. The Crustacea Decapoda Brachyura of Chile. Rev. Lund Univ. Chile Exped. 1948-49. 25: 1-128.

1960. Distribution and affinities of the brachyuran Crustacea. The biogeography of Baja California and adjacent areas. Part 2. Marine Biotas. Syst. Zool. 19: 105-123.

GEISTER, J. 1977. Occurrence of *Pocillopora* in Late Pleistocene Caribbean coral reefs. Second Intern. Symposium sur les coreaux et récifs corallines fossiles. Paris, September 1975. B.R.G.M. (Paris) Mem. 81: 378-388.

GEITZENAUER, K. R., M. B. ROCHE, AND A. MCINTYRE. 1979. Modern Pacific coccolith assemblages: derivation and application to Late Pleistocene paleotemperature analysis, p. 423-448.

GEORGE, R. Y. 1977. Dissimilar and similar trends in Arctic and Antarctic marine benthos, p. 391-408. *In* M. J. Dunbar [ed.] Polar oceans. Arctic Inst. N. Am. 681 p.

GERTH, H. 1925. Die Bedeutung der Tertiären Riffkovallenfauna des Malayischen Archipels fur die Entwicklung der lebenden Riffauna im Indopazifischen und Atlantischen Gebiet. Verhdl. Geol Mignb. Genootsch Nederland es Kolon. (Geol.) 8: 72-84 p.

GLEASON, H. A. 1922. On the relation between species and area. Ecology 3: 158-162.

GOLIKOV, A. N. 1982. O printsipakh raionirovaniya i unifikatsii terminov u morskoi biogeograffi. [On the principles of zoning and standardization of terms in marine biogeography], p. 94-99. *In* O. G. Kassakin and A. I. Kafanov [ed.] Morskaya biogeografiya: predmet, metody, printsipy rayonirovaniya. [Marine biogeography: subject matter, methods, principles of zoning]. Nauka. Moscow. 311 p. (Can. Transl. Fish. Aquat. Sci. 5054, 1984).

GOOCH, J. L., AND T. J. M. SCHOPF. 1972. Genetic variability in the deep sea: relative to environmental variability. Evolution 26: 545–552.

GORDON, W. A. 1974. Physical controls on marine biotic distribution in the Jurassic Period, p. 136–147. *In* C. C. Ross [ed.] Paleogeographic Provinces and Provinciality. Soc. Econ. Paleont. Miner. Spec. Publ. 21: 223 p.

GUNTHER, A. 1868. An account of the fishes of the states of Central America. Trans. Zool. Soc. 6: 377–494.

HAFLINGER, K. 1981. A survey of benthic infaunal communities of the southeastern Bering Sea shelf, p. 1091–1103. *In* D. W. Hood, J. A. Calder [ed.] The Eastern Bering Sea Shelf: oceanography and resources. Univ. Washington Press 2: 1339 p.

HALL, C. A. 1964. Shallow water marine climatic and molluscan provinces. Ecology 45: 226–234.

HALLAM, A. 1965. Observations on marine Lower Jurassic stratigraphy of North America, with special reference to the United States. Bul. Am. Assoc. Pet. Geol. 49: 1485–1501.

1978. How rare is phyletic gradualism and what is its evolutionary significance? Evidence from Jurassic bivalves. Paleobiology 4: 16–25.

HAYDEN, B. P., AND R. DOLAN. 1976. Coastal marine fauna and marine climates of the Americas. J. Biogeogr. 3: 71–81.

HECHT, A. D., AND B. AGAN. 1972. Diversity and age relationships in Recent and Miocene bivalves. Syst. Zool. 21: 308–312.

HECK, K. L., AND E. D. MCCOY. 1978. Long-distance dispersal and the reef-building corals of the Eastern Pacific. Mar. Biol. 48: 349–356.

HEDGPETH, J. W. 1957. Marine biogeography, p. 359–382. *In* Hedgepeth, J. W. [ed.] Treatise on marine ecology and paleoecology. Geol. Soc. Am. Mem. 67: 1296 p.

HEEZEN, B. C., C. D. HOLLISTER, AND W. F. RUDDIMAN. 1966. Shaping of the continental rise by deep geostrophic contour currents. Science 152: 502–508.

HERM, D. 1969. Marines pliozän und pleistozän in Nord. und mittel- Chile unter besonderen Berücksichtigung der entwicklung des molluskeu faune zitteliana, Abhandl. Bayer. Statsaml. Paläont U Histor. Geol. 2: 1–159, 18 kls.

HERRON, E. M., J. F. DEVEY, AND W. C. PITTMAN. 1974. Plate tectonics model for the evolution of the Arctic. Geology (August 1974): 377–380.

HERTLEIN, L. G. 1932. Mollusks and barnacles from Malpello and Cocos Islands. Nautilus 46: 43–45.

1937. A note on some species of marine mollusks occurring in both Polynesia and Western America. Proc. Am. Philos. Soc. 78: 303–312, pl. 1.

1972. Pliocene fossils from Baltra (South Seymour) Island, Galapagos Islands. Proc. Calif. Acad. Sci. 39: 25–46.

HERTLEIN, L. G., AND E. C. ALLISON. 1966. Additions to the molluscan fauna of Clipperton Island. Veliger 9: 138–140.

HERTLEIN, L. G., AND W. K. EMERSON. 1953. Mollusks from Clipperton Island (Eastern Pacific) with the description of a new species of gastropod. Trans. San Diego Soc. Nat. Hist. 11: 347–364.

HERTLEIN, L. G., AND A. M. STRONG. 1939. Marine Pleistocene mollusks from the Galapagos Islands. Proc. Calif. Acad. Sci. 23: 367–380, pl. 32.

1955. Marine mollusks collected at the Galapagos Islands during the voyage of the Velero III, 1931–1932. Essays in the natural sciences in honor of Capt. Allan Hancock. Univ. S. Calif. (Los Angeles): 111–145, pl. 1.

HESSLER, R. R., AND H. L. SANDERS. 1967. Faunal diversity in the deep-sea. Deep-Sea Res. 14: 65–78.

HILL, D. 1973. Lower Carboniferous corals, p. 133–142. *In* A. Hillman [ed.] Atlas of palaeobiogeography. Elsevier Sci. Publ. Amsterdam. xii + 531 p.

HOLDEN, J. C., AND R. S. DIETZ. 1972. Galapagos Gore, NaxCoPac triple junction and Carnegie/Cocos Ridges. Nature 235: 266–269.

HOPKINS, D. M. 1959. Cenozoic history of the Bering Land Bridge. Science 1519–1528.

1979. Landscape and climate of Beringia during Late Pleistocene and Holocene times, p. 15–41. *In* W. S. Laughlin, and A. B. Harper [ed.] The first Americans: origins, affinities, and adaptations. Gast. Fischer. New York.

HOPKINS, D. M. AND L. MARINCOVICH. 1984. Whale biogeography and the history of the Arctic Basin. Works of the Arctic Center. Groningen Rijksuniversitet 8: 7–24.

HOWELL, J. T. 1941. Hugh Cuming's visit to the Galapagos Islands. Lloydia 4: 291–292.

HSU, K. J. 1984. The Mediterranean was a desert. Princeton Univ. Press, 197 p.

HUTCHINS, L. W. 1947. The bases for temperature zonation in geographical distribution. Ecol. Monogr. 17: 325–335.

IHERING, H. VON. 1907. Les mollusques fossiles du Tertiaire et du Crétacé Supérieur de l'Argentine. An. Mus. Nac. Buenos Aires. (Ser. 3) 7: xiii + 611 p., 18 pls.

IMLAY, R. W. 1965. Jurassic marine faunal differentiation in Northern America. J. Paleontol 39: 1023–1038.

ITOIGAWA, J. 1978. Evidence of subtropical environments in the Miocene of Japan. Bull. Mizunami Fossil Mus. 5: 7–22.

JABLONSKI, D. 1980. Apparent vs. real biotic effects of transgressions and regressions. Paleobiology 6: 397–407.

JABLONSKI, D., AND J. W. VALENTINE. 1981. Onshore-offshore gradients in Recent Eastern Pacific shelf faunas and their paleobiogeographic significance, p. 441–453. *In* G. C. E. Scudder, and J. L. Reveal [ed.] Evolution Today. Proc. 2nd Int. Congr. systematic and evolutionary biology.

JABLONSKI, D., J. J. SEPKISKI, D. J. BOTTJER, AND P. M. SKEEHAN. 1983. Onshore–offshore patterns in the evolution of Phanerozoic shelf communities. Science 222: 1123–1125.

JACKSON, J. B. C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. Am. Nat. 108: 541–560.

JAMES, M. J. 1984. A new look at evolution in the Galapagos: evidence from the Late Cenozoic marine molluscan fauna. Biol. J. Linnean Soc. 21: 77–95.

JOHNSON, J. G. 1982. Occurrence of phyletic gradualism and punctuated equilibria through geologic time. J. Paleontol. 56: 1329–1331.

KAFANOV, A. I. 1982. Kainozoiskaya istoria malakofauni shel'fa severnoi Patsifiki [Cenozoic history of the molluscan faunas of the North Pacific shelf], p. 134–176. *In* O. G. Kassakin, and A. I. Kafanov [ed.] Morskaya biogeografiya: predmet, metody, printsipy rayonirovaniya. [Marine biogeography: subject matter, methods, principles of zoning.] Nauka. Moscow. 311 p. (Can. Transl. Fish. Aquat. Sci. 5052, 1984).

KALJO, D., AND E. KLAAMANN. 1973. Ordovician and Silurian corals, p. 37–45. *In* Hallam A. [ed.] Atlas of palaeobiogeography. Elsevier Sci. Publ. Amsterdam. xii + 531 p.

KARLSTROM, T. N. V. 1966. Quaternary glacial record of the North Pacific region and world-wide climatic changes, p. 153–182. *In* D. I. Blumenstock [ed.] Pleistocene and Post-Peistocene climatic variations in the Pacific areas. Honolulu Bishop. Mus. Res. 182 p.

KAY, E. A. 1967. The composition and relationships of the marine molluscan fauna of the Hawaiian Islands. Jpn. J. Malacol. 25: 96–104.

1979. Hawaiian marine shells. Reef and shore fauna of Hawaii. 4. Mollusca. Bernice P. Bishop Mus. Spec. Publ. 64: 653 p.

KEEN, A. M. 1971. Sea shells of Tropical West America. Second edition with assistance of James J. McLean. Stanford Univ. Press, 1064 p.

KEEN, A. M., AND E. COAN. 1975. Sea Shells of Tropical West America: additions and corrections to 1975. West. Soc. Malacol. Occas. Paps. 1: 66 p.

KEIGWIN, L. G. 1978. Pliocene closing of the Isthmus of Panama based on biostratygraphic evidence from nearby Pacific Ocean and Caribbean Sea Cores. Geology 6: 630–634.

KENNEDY, G. L. 1982. Historical evolution and application of the Pleistocene province concept along the eastern Pacific margin of North America. West. Soc. Malacol. Ann. Rep. 14: 14–15.

KENNEDY, G. L., K. R. LAJOIE, AND J. F. WEHMILLER. 1982. Aminostratigraphy and faunal correlations of the late Quarternary marine terraces, Pacific Coast, USA. Nature 299: 545–547.

KERR, R. A. 1987. Tracking the wandering poles of ancient earth. Science 236: 147–148.

KILMER, F. H. 1978. History of the Pliocene molluscan fauna of Northern Japan. Veliger 21: 227–231.

KNOX, G. A. 1960. Littoral ecology and biogeography of the Southern oceans. Proc. Roy. Soc. London 152 B: 577–624.

KNUDSEN, J. 1970. The systematics and biology of abyssal and hadal bivalvia. Galathea Rep. 11: 241 p., 20 pls.

KOHN, A. J. 1983. Marine biogeography and evolution in the tropical Pacific: zoological perspectives. Bull. Mar. Sci. 33: 528–535.

KRISHTOFOVICH, L. V. 1964. Mollyuski tretichnykh otlozhenii Sakhalina [The molluscs of the Tertiary deposits of Sakhalin] Trudy vsesoyuz. neft. nr-i geol-razved. in-ta. 232: 343 p.

KURONUMA, K. 1942. Latitudinal value: a quantitative indication of fish distribution, and its application to the flatfish of Japanese islands. Bull. Biogeogr. Soc. Jpn. 12: 85–91.

KURTEN, B. 1972. The ice-age. Rupt. Hart-Davis London. 230 p.

LADD, H. S., J. I. TRACEY, AND M. G. GROSS. 1967. Drillings on Midway Atoll, Hawaii. Science 156: 1088–1095.

LAMY, E. 1933. Les idées d'A. d'Orbigny et celles de H. von Ihering sur la distribution géographique des mollusques marines côtiers de l'Amérique Méridionale. Commémoration du voyage d'Alcide d'Orbigny en Amérique du Sud (1826–1837). Masson et Cie., Paris. 27–41.

1936. Liste des mollusques recueillis par la mission Franco-Belge à l'Île de Pâques (1934). Bull. Mus. Hist. Nat. Paris (Series 2) 8: 267–268.

1938. Mollusques recueillis à l'Île de Pâques par la mission Franco-Belge (1934). J Conchyliol. 82: 131–143.

LELOUP, E. 1956. Polyplacophora. Rep. Lund Univ. Chile Exped. 1948–49. 27: 1–95.

LEVINGTON, J. 1973. Genetic variation in a gradient of environmental variability: marine Bivalvia (Mollusca). Science 180: 75–76.

1974. Trophic group and evolution in bivalve molluscs. Palaeontology 17: 579–585.

LEVITUS, S. 1982. Climatological atlas of the world ocean. United States National Oceanic and Atmospheric Administration. Professional Paper 13: 173 p.

LOCZY, L. DE. 1971. Gondwana problems in the light of recent paleontologic and tectonic recognitions. An. Acad. Bras. Cienc. 43 (Suppl.): 363–386.

MACARTHUR, J. W. 1975. Environmental fluctuations and species diversity, p. 74–80. *In* M. L. Cody and J. M. Diamond [ed.] Ecology and evolution of communities. Belknap Press, Harvard Univ. 545 p.

MCCOY, F. W., AND C. SANCETTA. 1985. North Pacific sediments, p. 1–64. *In* E. M. Noirn, F. G. Stehli, and S. Uyeda [ed.] The ocean basins and margins. Vol. 7A The Pacific Ocean. Plenum Press, New York, NY. 733 p.

MCDONALD, J., H. M. FEDER, AND M. HOBERG. 1981. Bivalve mollusks of the Southeastern Bering Sea, p. 1155–1204. *In* D. W. Hood, J. A. Calder [ed.] The Eastern Bering Sea Shelf: oceanography and resources. Univ. Washington Press 2: 1339 p.

MCGUINNESS, K. A. 1984. Equations and explanations in the study of species-area curves. Biol. Rev. 59: 423–440.

MCKINNEY, M. L. 1985. Distinguishing patterns of evolution from patterns of deposition. J. Paleontol. 59: 561–567.

MADSEN, F. J. 1956. Asteroidea. Rep. Lund Univ. Chile Exped. 1947–49. 24: 53 pp.

MALMGREN, B. A., AND J. P. KENNETT. 1981. Phyletic gradualism in Cenozoic planktonic foraminiferal lineage, DSDP Site 284, southeast Pacific. Paleobiology 7: 230–240.

MANN, G. F. 1954. El mar Chileno y sus regiones biogeograficas. Invest. Zool. Chilenas 2: 75–86.

MARGOLIS, S. V., AND J. P. KENNETT. 1970. Antarctic glaciation during the Tertiary recorded in sub-Antarctic deep-sea cores. Science 170: 1085–1087.

MARINCOVICH, L. JR. 1973. Intertidal mollusks of Iquique, Chile. Nat. Hist. Mus. Los Angeles Sci. Bull. 16: 49 p.

MARINCOVICH, L. JR., E. M. BROWERS, AND D. M. HOPKINS. 1983. Paleogeographic affinities and endemism of Cretaceous and Paleocene marine faunas in the Arctic. U.S. Geological Survey Polar Research Symposium. Abst. U.S. Geol. Surv. Circ. 911: 45–46.

MARINCOVICH, L. JR., E. M. BROWERS, AND L. D. CARTER. 1985. Early Tertiary marine fossils from northern Alaska: implications for Arctic Ocean paleogeography and faunal evolution. Geology 13: 770–773.

MENARD, H. W., AND E. L. HAMILTON. 1963. Paleogeography of the Tropical Pacific, p. 118–232. *In* J. L. Gressit [ed.] Pacific Basin Biogeography Symposium. Bernice P. Bishop Mus. Honolulu. 345 p.

MENZIES, R. J., R. Y. GEORGE, AND G. T. ROWE. 1973. Abyssal environment and ecology of the world oceans. Wiley, New York, NY, 479 p.

MEYERHOFF, A. A. 1970. Continental drift: implications of paleomagnetic studies, meteorology, physical oceanography, and climatology. J. Geol. 78: 1–51.

MIDDLEMISS, F. A., AND P. F. RAWSON. 1971. Faunal provinces in space and time — some general considerations, p. 199–210. *In* F. A. Middlemiss, P. F. Rawson, and G. Newell [ed.] Faunal provinces in space and time. Proc. 17th Inter-Univ. Geol. Congr. Queen Mary College Univ. London. December 1969. Seel House London. 236 p.

MONTOYA, M. 1983. Los moluscos marinas de la Isla de Coco, Costa Rica. 1. Lista anotida de especies. Brenesia 21: 325–353.

MONTOYA, M., D. R. SHASKY, AND K. L. KAISER. 1988. The marine molluscs of Isla del Coco, Costa Rica (Draf).

MOORE, D. G. 1964. Acoustic-reflection reconnaissance of continental shelves: Eastern Bering and Chukchi Seas, p. 319–162. *In* R.L. Miller [ed.] Papers in marine geology, Shepard Commemorative volume. The Macmillan Co., 531 p.

MUROMTSEV, A. N. 1963. Atlas of temperature, salinity and density of water in the Pacific Ocean. Akad. Nauk. Moscow.

NEIMAN, A. A. 1963. Kolichestvennoye raspredeleniye bentosa na shel'fe i verkhnikh gorizontakh sklona vostochnoi chasti Beringova morya [Quantitative distribution of benthos on the continental shelf and upper horizon of the slope in the Eastern Bering Sea]. Trudy Moskva Vses n-issl. Inst. Morskogo rybnogo khoz i okeanograffi 48: 45–205.

NESIS, K. N. 1962. Tikhookeanskiye elementy v bentose severo-zapadnoy Atlantiki [Pacific elements in Northern Atlantic benthos]. Sov. Fish. Inst. N. W. Atlantic. VINRO-PINRO Moscow: 83–98.

NEWELL, I. M. 1948. Marine molluscan provinces of western North America: a critique and a new analysis. Proc. Am. Philos. Soc. 92: 155–166.

NEWELL, N. D. 1962. Paleontological gaps and geochronology. J. Paleontol. 36: 592–610.

1971. The outline history of tropical reefs. Am. Mus. Novit. 2465: 37 p.

NEWELL, N. D., AND D. W. BOYD. 1978. A palaeontologist's view of bivalve phylogeny. Phil. Trans. Roy. Soc. Can. 284: 203–215.

NEWMAN, W. A. 1979. California Transition Zone: significance of short-range endemics, p. 399–416. *In* J. Gray and A. J. Boucot [ed.] Historical biogeography, plate tectonics, and the changing environment. Oregon State Univ. Press, OR.

NICOL, D. 1966. Description, ecology, and geographic distribution of some Antarctic pelecypods. Bull. Am. Paleontol. 51: 1–102.

ODHNER, N. H. 1922. Mollusca from Juan Fernandez and Easter Island, p. 219–254. *In* C. Skottsberg [ed.] The natural history of Juan Fernandez and Easter Island. Almquist & Wiksells, Uppsala. 3 vols.

OLSSON, A. A. 1972. Origin of the existing Panamic molluscan biotas in terms of their geologic history and their separation by the Isthmian land barrier. Bull. Biol. Soc. Washington 2: 117–123.

ORBIGNY, A. D'. 1834–1847. Voyage dans l'Amérique Méridionale. Mollusques. Paris vol. 5: xliii + 758 p. atlas, 85 pls.

1845. Recherches sur les lois qui président à la distribution géographique des mollusques côtières marins. Am. Sci. Nat. Zool. (Ser. 3) 3: 193–221.

OSORIO, C., AND N. BAHAMONDE. 1970. Lista preliminar de Lamellibranchios del Chile. Boln. Mus. Nac. Nist. Nat. 31: 185–256.

OWEN, H. G. 1976. Continental displacement and expansion of the earth during the Mesozoic and Cenozoic. Phil. Trans. Roy. Soc. London 281A: 223–291.

OYAMA, K., A. MIZUNO, AND T. SAKAMOTO. 1960. Illustrated handbook of Japanese Paleocene molluscs. Geol. Surv. Japan, Tokyo. 244 p.

PAINE, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65–75.

PELSENEER, P. 1903. Résultats du voyage du S. Y. *Belgica* en 1897–1898–1899. Expédition Antarctique. Belge. Zoologie Mollusques. Buschmann, Brussels. 1–85, 9 pls.

PETERSEN, G. H., AND M. A. CURTIS. 1980. Differences in energy flow through major components of subarctic temperate and tropical marine shelf ecosystems. Dana 1 (0): 53–64.

PETUCH, E. J. 1982. Geographical heterochromy: comtemporaneous coexistence of Neogene of Recent molluscan faunas in America. Paleogeogr. Palaeoclimatol. Palaeoecol. 37: 277–312.

PIANKA, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100: 33–46.

PITMAN, W. C., R. L. LARSON, AND E. M. HERRON. 1974. The age of the ocean basin. Geol. Soc. Am. 2 charts, summary.

POJETA, J. 1971. Review of Ordovician pelecypods. U.S. Geol. Surv. Prof. Pap. 695: 45 p., 20 pls.

POSNER, G. S. 1957. The Peru Current. Bull. Bingham Oceanogr. Coll. 26: 106–155.

POWELL, A. W. B. 1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Rep. 26: 47–146.

1957. Marine provinces of the Indo West Pacific. Proc. 8th Pac. Sci. Congr. 3: 359–362.

1960. Antarctic and Subantarctic Mollusca. Rec. Auckland Inst. New Zealand 5: 117–193.

PRORINA, N. G. 1969. Molliuski srednemiotseiovykh otlozhenii keonotskoe raiona vostochnogo poberrezh'ya Kamchatki. [The molluscs of the Middle Miocene deposits of the Keonotskoe region of the east coast of Kamchatka]. Trans All-Union Inst. Petrol. Geol. Explor. 268: 244–269.

RAUP, D. M., AND J. SEPKOSKI. 1984. Periodicity of extinctions in the geologic past. Proc. Nat. Acad. Sci. U.S. 81: 801–805.

REHDER, H. A. 1980. The marine mollusks of Easter Island (Isla de Pascua) and Sala y Gomez. Smith. Contrib. Zool. 289: 167 p.

REID, J. L., E. BRINTON, A. FLEMINGER, E. L. VENRICK, AND J. A. MCGWANN. 1978. Ocean circulation and marine life, p. 65–130. *In* H. Charnock and G. Deacon [ed.] Advances in oceanography. Plenum Press, New York, NY.

REID, J. L., G. I. RODEN, AND J. G. WYLLIE. 1958. Studies of the California Current system. Calif. Co-op. Oceanic Fish. Invest. Prog. Rep. 6: 27–57.

ROHDE, K. 1978. Latitudinal gradients in species diversity and their causes. 1. A review of the hypotheses explaining the gradient. Zentralbl. Biol. 97: 393–403.

ROSS, A. 1962. Results of the Puritan-American Museum of Natural History expedition to West Mexico. 15. The littoral balanomorph Cirripedia. Am. Mus. Novit. 2084: 44 p.

ROSS, C. A. 1973. Carboniferous Foraminifera, p. 127–132. *In* A. Hallam [ed.] Atlas of palaeobiogeography. Elsevier Sci. Publ. Amsterdam. xii + 531 p.

ROSS, C. A., AND J. R. P. ROSS. 1981. Late Paleozoic faunas around the paleotropical margin, p. 425–440. *In* G. G. E. Scudder and J. L. Reveal [ed.] Evolution today. Proc. 2nd. Int. Congr. systematic and evolutionary biology.

ROWE, G. T. 1971. Benthic biomass and surface productivity, p. 441–454. *In* J. D. Costlow [ed.] Fertility of the sea. Gordon & Breach, New York, NY. 449 p.

1983. Biomass and production of the deep-sea macrobenthos, p. 97–122. *In* G.T. Rowe [ed.] The Sea. (Vol. 8): Deepsea biology, Wiley, New York, NY.

ROWE, G. T., P. T. POLLONI, AND S. HORNER. 1974. Benthic biomass estimates from the Northwestern Atlantic Ocean and the northern Gulf of Mexico. Deep-Sea Res. 21: 641–650.

ROZBACZYLO, N., AND J. C. CASTILLA. 1987. Invertebrados marinos del Archipielago du Juan Fernandez. Islas Oceanics Chileans. Univ. Cat. Chile: 167–184.

SAGER, W. W., AND U. BLEIL. 1987. Latitudinal shift of Pacific kotopots during the late Cretaceous and early Tertiary. Nature 326: 477–490.

SALVAT, B., AND J. P. EHRHARDT. 1970. Mollusques de l'Île Clipperton. Bull. Mus. Nat. Hist. Nat. 42: 223–231.

SALVAT, B., AND F. SALVAT. 1972. Geographic distribution of *Pinna rugosa* Sowerby, 1835 (Mollusca: Bivalvia) and its occurrence on Clipperton Island. Veliger 15: 43.

SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102: 243-282.

SANDERS, H. L., AND R. R. HESSLER. 1969. Ecology of the deep-sea benthos. Science 163: 1414-1424.

SAUSSAYE, M. PETIT DE LA. 1858. Des migrations et de la dispersion de certaines espèces de mollusques. J. Conchyliol 7: 105-118.

SAVIN, S. M., G. DOUGLAS, AND F. G. STEHLI. 1975. Tertiary marine paleotemperatures. Bull. Geol. Soc. Am. 86: 1499-1510.

SCARLATO, O. A., AND A. I. KAFANOV. 1976. Dopliotsenovaya fauna Polyarnogo'basseyna i vopovs o'iskhodnoi avtokhtonnosti zuarkticheskikh rodor. [The pre-Pliocene fauna of the Polar Basin and the question of the initial autochthonousness of the euarctic genera]. Zool. Zhurn. 55: 1765-1772.

SCHELTEMA, R. S. 1977. Dispersal of marine invertebrates and biostratigraphic implications, p. 73-108. *In* E. G. Kaufmann and J. E. Hazel [ed.] Concepts and methods of biostratigraphy. Dowden, Hutchinson, and Ross.

SCHELTEMA, R. S., AND I. P. WILLIAMS. 1983. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and Western Pacific mollusks. Bull. Mar. Sci. 33: 545-565.

SCHENCK, H. G. 1937. An index method for comparing molluscan faunules. Proc. Am. Philos. Soc. 77: 161-182.

1945. Geological application of biometrical analysis of molluscan assemblages. J. Paleont. 19: 504-521.

SCHENCK, H. G. AND A. M. KEEN. 1936. Marine molluscan provinces of western North America. Proc. Am. Philos. Soc. 76: 921-938.

1940. Biometrical analysis of molluscan assemblages. Mem. Soc. Biogeogr. Paris 7: 379-392.

SCHILDER, F. A. 1965. The geographical distribution of cowries (Mollusca: Gastropoda). Veliger 7: 171-183.

SCHOPF, T. J. M. 1979. The role of biogeographic provinces in regulating marine faunal diversity through geologic time, p. 449-459. *In* J. Gay and A. J. Boucot [ed.] Historical biogeography, plate tectonics, and the changing environment. Biol. Colloq. Oregon State Univ. 1980. Paleoceanography. Harvard Univ. Press. 341 p.

SCHOPF, T. J. M., J. B. FISHER, AND C. A. F. SMITH. 1978. Is the marine latitudinal diversity gradient merely another example of the species area curve? p. 365-386. *In* J. Beardmore and B. Battaglio [ed.] Genetics, ecology and evolution of marine organisms. Plenum Press, New York, NY.

SCHWENGEL, J. 1938. Zoological results of the George Vanderbilt South Pacific Expedition 1937. Part 1. Galapagos Mollusca. Proc. Acad. Nat. Sci. Philadelphia 90: 1-3.

SCHWIDERSKI, E. W. 1979. Global ocean tides. Part 2. The semidiurnal principal lunar tide (M2), Atlas of tidal charts and maps. U.S. Naval Surface Weapons Centre NSWC TR 79-414.

SEMENOV, V. N. 1964. Quantitative distribution of benthos on the shelf of the southeastern Bering Sea, p. 167-175. *In* Moiseev P. A. [ed.] Soviet fisheries investigations in the northeastern Pacific. (Israel Prog. Sci. Transl. 1968).

1982. Biogeografisheskoe raionirovanie shel'fa yuzknoi Ameriki no osnove klassifikatsii vidovykh arealov donnykh bespozvonochnykh. [The biogeographic zonation of the South American shelf based on a classification of the ranges of bottom-dwelling invertebrate species], p. 184-269. *In* Kafanov A. I. [ed.] Morskaya biogeografiya: predmet, metody, printsipy raionirovaniya. Nauk. Moscow. SSSR. 311 p. (Canadian Transl. Fish. Aquat. Sci. 5071, 1984).

SEPKOSKI, J. J. 1987. Environmental trends in extinction during the Paleozoic. Science 235: 64-65.

SERGEEV, K. F. 1976. Tektonika kuril'skoii ostrovnoii systemy. [The tectonics of the Kurile Islands system] Nauk Press Moscow. 240 p.

SETCHELL, W. A. 1920. Stenothermy and zone-invasion. Am. Nat. 54: 385-397.

SHUTO, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. Lethaia 7: 239-256.

SIEVERS, H. A., AND N. S. SANDOVAL. 1975. Masas de agua y circulacion en el Oceano Pacifico sudoriental. Latitudes 18°S-33°S. (Operation oceanografica "Marchile VIII"). Cienc. Tech. Mar. Contrib. CONA 1: 7-67.

SIMBERLOFF, D. S. 1969. Community effects of introduced species, p. 53-81. *In* N. H. Nitechi [ed.] Biotic crises in ecological and evolutionary time. Academic Press, New York, NY.

SKEVINGTON, D. 1973. Ordovician graptolites, p. 27-53. *In* A. Hallam [ed.] Atlas of palaeobiogeography. Elsevier Sci. Pub. Amsterdam. xii + 531 p.

SMITH, A. G., AND J. C. BRIDEN. 1977. Mesozoic and Cenozoic paleocontinental maps. Cambridge Univ. Press. 10 p., 52 maps.

SMITH, E. A. 1877. Account of the zoological collections made during the visit of H.M.S. "Petel" to the Galapagos Islands. Mollusca. Proc. Zool. Soc. London (for 1877): 69-783, 91-93.

SMITH, J. P. 1904. Periodic migrations between the Asiatic and American coasts of the Pacific Ocean. Am. J. Sci. (Ser. 4) 17: 217-233.

SMITH, J. T. 1983. Tertiary molluscan distributions from Baja California Sur, Mexico. Am. Malacol. Bull. 2: 84-85.

1984. Miocene and Pliocene marine mollusks and preliminary correlations, Viscaino Peninsula to Aroyo La Prisima, northwestern Baja California Sur, Mexico, p. 197-217. *In* V. A. Frizzell [ed.] Geology of the Baja California Peninsula. Pacific Section S.E.P.M. 39.

1986. Applied malacology: new molluscan data on the evolution of the Gulf of California and Baja California peninsula, Mexico. A.M.V. Aust. 4: 238-239.

SOHL, N. F. 1977. Utility of gastropods in biostratigraphy, p. 519-539. *In* E. G. Kaufmann and J. E. Hazel [ed.] concepts and methods of biostratigraphy. Dowden and Ross, Pennsylvania.

SOKOLOVA, M. N. 1972. Trophic structure of deep-sea macrobenthos. Mar. Biol. 16: 1-12.

SOOT-RYEN, T. 1957. On a small collection of Pelecypoda from Peru to Panama. Lunds Univ. Arss. (Ser. 2) 55: 1-86.

SPARKS, A. K., AND W. T. PEREYRA. 1966. Benthic invertebrates of the S. E. Chukchi Sea, p. 817-838. *In* N. J. Wilmovsky [ed.] Environment of the Cape Thompson Region, Alaska. U.S. Atomic Energy Com. Washington.

SPRINGER, V. G. 1982. Pacific plate biogeography, with special reference to shorefishes. Smith. Contrib. Zool. 367: 182 p.

STEARNS, R. C. E. 1893. Scientific results of exploration by the U.S. Fish. Commission's steamer "Albatross". No 25. Report on the mollusk-fauna of the Galapagos Islands with descriptions of new species. Proc. U.S. Nat. Mus. 16: 353-450, pls 51, 52.

STEELE, P. H. 1957. Easter Islands shells. Nautilus 70: 111-113.

STEHLI, F. G. 1964. Permian zoogeography and its bearing on climate, p. 537-549. *In* A. E. M. Nairn [ed.] Problems in palaeoclimatology. Proc. NATO Palaeoclimat. Conf. 1963. Interscience, London. xiii + 705 p.

STEHLI, F. G., R. G. DOUGLAS, AND N. D. NEWELL. 1969. Generation and maintainance of gradients in taxonomic diversity. Science 164: 947-949.

STEHLI, F. G., A. L. MCALESTER, AND C. E. HELSLEY. 1967. Taxonomic diversity of recent bivalves and some implications for geology. Geol. Soc. Am. Bull. 78: 455-466.

STEMPELL, W. 1902. Die Muscheln der Sammlung Plate. (Systematische Uebersicht), p. 217-249, pl. 12. *In* Plate L. Fauna Chilensis. Zool. Jarb. Suppl. 5.

STEPHENSON, A., AND A. A. STEPHENSON. 1961. Life between tidemarks in North America. IV. Vancouver Island. J. Ecol. 49: 227-243.

STOKER, S. 1981. Benthic invertebrate macrofauna of the Eastern Bering/Chukchi Continental shelf, p. 1069-1090. *In* D. W. Hood and J. A. Calder [ed.] The Eastern Bering Sea shelf: oceanography and resources. Univ. Washington Press, Vol. 2: 1339 p.

STRATHMANN, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Ann. Rev. Ecol. Syst. 16: 339-361.

STRONG, A. M. 1954. The marine molluscan fauna of Guadalupe Island, Mexico. Min. Conch. Club S. Calf. 142: 6-10.

STRONG, A. M., AND G. D. HANNA. 1938a. Marine Mollusca of Guadalupe Island, Mexico. Proc. Calif. Acad. Sci. 19: 1-6.

1938b. Marine Mollusca of Revillagigedo Island, Mexico. Proc. Calif. Acad. Sci. 19: 7-12.

STUARDO, J. 1964. Distribution de los moluscos marinos litorales en latinoamerica. Inst. Biol. Mar. Argentina. 7: 74-91.

SVENSON, H. K. 1946. Vegetation of the coast of Ecuador and Peru and its relation to the Galapagos Islands. Am. J. Bot. 33: 394-427.

SWEET, W. C., AND S. R. BERGSTROM. 1974. Provincialism exhibited by Ordovician Conodont faunas, p. 189-202. *In* C. A. Ross [ed.] Paleogeographic provinces and provinciality. Soc. Econ. Paleont. Miner. Spec. Publ. 21: 233 p.

SYLVESTER-BRADLEY, P. C. 1971. Dynamic factors in animal palaeogeography, p. 1-18. *In* F. A. Middlemiss, P. F. Rawson, and G. Newell [ed.] Faunal Provinces in space and time. Steel House Press, Liverpool. 236 p.

TABATA, S. 1975. The general circulation of the Pacific Ocean and a brief account of the oceanographic structure of the North Pacific Ocean. Part 1. Circulation and volume transports. Atmosphere 13: 133-168.

1976. Evidence of a westward-flowing 'Subarctic Countercurrent' in the North Pacific Ocean. J. Fish. Res. Board Can. 33: 2168-2196.

TAKAI, F., T. MATSUMOTO, AND R. TORIYAMA. 1963. Geology of Japan. Univ. Cali. Press, Berkeley, CA. 279 p.

TANNER, W. F. 1968. Tertiary sea level symposium — Introduction. Palaegeogr. Palaeoclimatol. Palaeoecol. 5: 7-14.

TAVIANI, M. 1979. I Molluschi raccolti dalla spedizione 'L.Mares-G.R.S.T.S.' alle isole Galapagos. 1. Gastropodae Bivalvia. Mus. Zool. Univ. Firenze. 61 p.

TAYLOR, M. E. 1977. Late Cambrian of western North America: Trilobite biofacies, environmental significance, and biostratigraphic implications, p. 307-425. *In* E. G. Kauffmann and J. E. Hazel [ed.] Concepts and methods of biostratigraphy. Dowden, Hutchinson and Ross, Pennsylvania. 658 p.

TIPTON, A., R. M. KLEINFELL, AND D. W. WEAVER. 1974. Oligocene biostratigraphy, San Joaquin Valley. Calif. Univ. Publ. Geol. Sci. 105: 1-81.

USHAKOV, P. V. 1952. Chukotskoe morei i ego donnai fauna. [Chukchi Sea and its bottom fauna]. Krainii Severo-Vostok Soiuza, SSSR. Akad. Nauk. 2: 5-82.

VAIL, P. R., R. M. MITCHUM, AND S. THOMPSON. 1977. Seismic stratigraphy and global changes of sea level. Part 4. Global cycles of relative changes of sea level. *In* C. E. Payton [ed.] Seismic stratigraphy: applications to hydrocarbon exploration. Mem. Am. Assoc. Petrol. Geol. 26: 83-97.

VALENTINE, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11: 198-212.

1971. Plate tectonics and shallow marine diversity and endemism, an actualistic model. Syst. Zool. 20: 253-264.

VALENTINE, J. W., AND E. M. MOORES. 1972. Global tectonics and the fossil record. J. Geol. 80: 167-184.

VERMEIJ, G. J. 1978. Biogeography and adaptation. Harvard Univ. Press 332 p.

VINOGRADOVA, N. G. 1959. The zoogeographical distribution of the deep-water bottom fauna in the abyssal zone of the ocean. Deep-Sea Res. 5: 205-208.

1962. Vertical zonation in the distribution of deep-sea benthic fauna in the ocean. Deep-Sea Res. 8: 245-250.

VINTON, K. W. 1951. Origins of life on the Galapagos Islands. Am. J. Sci. 249: 356-376, pls. 1,2.

VIVIANI, C. A. 1975. Communicades marinas litorales. Publ. Occas. Lab. Ecol. Marina Iquique. 196 p. (Mimeo)

1979. Ecogeografia del litoral Chileno. Stud. Neotrop. Fauna Environ. 14: 65-123.

WALKER, B. W. 1960. The distribution and affinities of the marine fish fauna of the Gulf of California. The biogeography of Baja California and adjacent seas. Syst. Zool. 9: 123-133.

WALLACE, A. R. ,1876. The geographical distribution of animals, with a study of the relations of living and extinct faunas as elucidating past changes of the earth's surface. 2 vol. MacMillan, London. 110 p.

1878. Tropical nature and other essays. MacMillan, London. 356 p.

1880. Island Life: or the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. MacMillan, London. 526 p.

WATERHOUSE, J. B., AND G. BONHAM-CARTER. 1975. Global distribution and character of Permian biomes based on brachipod assemblages. Can. J. Earth Sci. 12: 1085-1146.

WATKINS, R. 1974. Molluscan paleobiology of the Miocene Wimer Formation, Del Norte County, California. J. Paleontol. 48: 1264-1282.

WEBB, W. L. 1950. Biogeographic regions of Texas and Oklahoma. Ecology 31: 426-433.

WELDEN, C. W., AND W. L. SLAUSON. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quart. Rev. Biol. 61: 23-44.

WHITTINGTON, H. B. 1973. Ordovician trilobites, p. 13-18. *In* A. Hallam [ed.] Atlas of palaeobiogeography. Elsevier Sci. Pub. Amsterdam. xii + 531 p.

WILLIAMS, C. B. 1964. Patterns in the balance of nature. Academic Press. London, 324 p.

WILLIAMSON, M. H. 1978. The ordination of incidence data. J. Ecol. 66: 911-920.

WIMMER, A. 1879. Zur Conchylia-Fauna der Galapagos-Inseln. Sbr. Akad. Wiss. Wien. (Mat-nat Kl. Abt. 1) 80: 465-514.

WISHNER, K. F. 1980. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Res. 27: 203-216.

WOLFE, J. A., AND D. M. HOPKINS. 1967. Climatic change recorded by Tertiary land floras in northwestern North America, p. 67–76. *In* K. Hatai [ed.] Tertiary correlations of climatic changes in the Pacific. 11th Pac. Sci. Congr. Tokyo.

WOODRING, F. P. 1966. The Panama land bridge as a sea barrier. Proc. Am. Philo. Soc. 110: 425–433.

1974. The Miocene Caribbean faunal province and its subprovinces. Verhandl. Naturf. Ges. Basel. 84: 209–213.

WYRTKI, K. 1965. Summary of the physical oceanography of the East Pacific Ocean. Univ. Calif. IMR.65-10: 40 p.

XU, B. 1985. Discussion on paleobiomigration and associated problems. Sci. Sinica. 28B: 772–784.

ZENKEVICH, L. A. 1949a. La structure biologique de l'océan. CR. 13 Congr. Inter. Zool. 522–529.

1949b. Sur l'ancienneté de l'origine de la faune marine d'eau froide. CR. 13 Congr. Inter. Zool. 550.

1963. Biology of the seas of the USSR. George Allen and Unwin. London. 955 p.

ZIEGLER, A. M., K. S. HANSEN, M. E. JOHNSON, M. A. KELLY, C. R. SCOTESE, AND R. VAN DER VOO. 1977. Silurian continental distribution, paleogeography, climatology, and biogeography. Tectonophysics 40: 13–51.

ZINSMEISTER, W. J. 1978. Effect of formation of the west Antarctic ice sheet on shallow-water marine faunas of Chile. Antarctic J. 13: 25–26.

APPENDICES

Appendix 1

Bathymetric and geographic ranges of the genera of Bivalvia in the eastern Pacific Ocean.

Genus	Range		Depth (m)	Epoch*
Abra	52°N	9°N	20–3932	Recent
Acesta	37°N	53°S	450–2200	Recent
Acharax	57°N	12°S	800–3000	Recent
Acila	57°N	28°N	5–200	Miocene
Acrosterigma	26°N	1°S	Int–10	Recent
Adontorhina		34°N	70–800	Pleistocene
Adrana	31°N	14°S	2–55	Recent
Adula	49°N	5°S	Int	Recent
Agerostea	28°N	5°S	5–20	Pliocene
Agriodesma	56°N	4°S	Int–40	Recent
Aligena	31°N	3°S	Int–25	Pleistocene
Ameghinoma	33°S	54°S	Int–5	Pliocene
Americardia	34°N	5°S	Int–155	Pliocene
Americina	31°N	12°N	Int–25	Recent
Amiantis	35°N	23°N	1–20	Miocene
Amphichaena	17°N	13°N	Int	Recent
Anadara	34°N	5°S	Int–130	Miocene
Anatina	27°N	2°S	20–50	Recent
Anomia	37°N	5°N	Int–130	Pliocene
Arca	28°N	33°S	Int–150	Pliocene
Arcinella	28°N	6°N	25–80	Pliocene
Arcopsis	29°N	9°S	Int	Pliocene
Argopecten	30°N	55°S	Int–150	Pliocene
Astarte	73°N	48°N	Int–500	Pliocene
Asthenothaerus	34°N	23°N	2–50	Recent
Atrina	34°N	5°S	2–30	Pliocene
Bankia	55°N	54°S	Int–90	Recent
Barbatia	34°N	52°S	Int–120	Pliocene
Barnea	46°N	54°S	Int–30	Pleistocene
Basterotia	24°N	1°S	Int–45	Pliocene
Bathyarca	49°N	33°S	2030–3814	Recent
Bernardina	37°N	21°N	20–80	Pleistocene
Brachidontes	34°N	54°S	Int	Pliocene
Bushia		8°N	93	Recent
Calyptogena	53°N	1°N	500–2690	Recent
Cardiomya	60°N	1°S	15–2200	Recent
Cardia	29°N	4°S	Int–27	Pliocene
Carditamera	23°N	1°S	Int–25	Pleistocene
Carditella	24°S	55°S	Int–260	Recent
Cardites	30°N	4°S	Int–30	Pleistocene
Carditopsis	54°N	33°S	10–150	Recent
Chaceia	37°N	28°N	Int–2	Pliocene
Chama	44°N	5°S	Int–100	Pleistocene
Chione	34°N	54°S	Int–80	Pliocene
Chlamydoconcha	38°N	27°N	Int–40	Recent
Chlamys	72°N	53°S	Int–300	Miocene
Choromytilus	55°S	6°S	Int–5	Pleistocene
Clementia	28°N	0	5–20	Pliocene
Clinocardium	71°N	33°N	Int–150	Miocene
Codakia	9°N	1°S	Int–5	Recent
Compsomyax	61°N	28°N	2–550	Miocene
Conchocele	60°N	43°N	50–2050	Oligocene
Condylocardia	24°N	7°N	Int–400	Pleistocene
Cooperella	40°N	9°N	10–80	Pleistocene
Corbula	37°N	14°S	Int–100	Miocene
Crassicardia	71°N	51°N	1–200	Pliocene
Crassinella	34°N	4°S	Int–160	Pliocene
Crassostrea	60°N	42°S	Int	Pliocene
Crenella	60°N	2°S	5–400	Pliocene
Cryptomya	60°N	5°S	Int–80	Miocene
Ctena	31°N	2°S	Int–120	Pliocene
Cumingia	42°N	42°S	Int–65	Miocene

Appendix 1 (*Continued*)

Genus	Range		Depth (m)	Epoch*
Cuspidaria	71°N	50°S	20–5307	Recent
Cyamiocardium		42°S	15	Recent
Cyathodonta	34°N	4°S	Int–110	Pliocene
Cyamium	5°N	54°S	150–250	Recent
Cyamiomactra		33°S	20	Recent
Cyclinella	27°N	33°S	Int–50	Pleistocene
Cyclocardia	71°N	35°S	1–2211	Pliocene
Cyclopecten	49°N	52°S	2–3670	Recent
Cymatioa	28°N	3°S	Int–45	Recent
Cymatoica	24°N	2°S	5–40	Recent
Cyrtodaria	71°N	64°N	25–50	Pliocene
Cyrtopleura	28°N	4°S	Int–30	Pleistocene
Dacrydium	55°N	8°S	45–3670	Recent
Delectopecten	58°N	28°N	50–2000	Pliocene
Dimya	34°N	29°N	85–1250	Recent
Diplodonta	71°N	3°N	Int–140	Pleistocene
Diplodontina		52°S	Int–50	Recent
Diplothyra	30°N	17°N	Int–18	Recent
Divalinga	25°N	5°S	Int–55	Pliocene
Donax	33°N	34°S	Int–25	Pleistocene
Dosinia	28°N	6°S	Int–80	Pliocene
Empleconia	57°N	54°N	400–650	Recent
Entodesma	37°N	46°S	Int–40	Recent
Ensis	37°N	54°S	Int–50	Pleistocene
Ensitellops	31°N	2°S	Int–120	Recent
Erycina	32°N	33°S	1–10	Recent
Ervilia	34°N	33°S	Int–35	Recent
Eucrassatella	30°N	5°S	10–55	Pliocene
Eurhomalea	4°S	54°S	Int–150	Recent
Felaniella	37°N	42°S	Int–75	Oligocene
Fugleria	29°N	4°S	Int–70	Pliocene
Gaimardia	25°S	54°S	Int–150	Recent
Galeommella	31°N	3°S	Int–15	Recent
Gari	60°N	45°S	Int–170	Pliocene
Gastrochaena	28°N	12°S	Int–30	Recent
Gemma		33°N	Int	Recent
Glans	58°N	28°N	Int–100	Recent
Glycymeris	60°N	6°S	Int–250	Pliocene
Gouldia	26°N	8°N	80–160	Recent
Gregariella	37°N	13°S	Int–100	Recent
Grippina	33°N	24°N	5–100	Recent
Halicardia	59°N	1°S	135–1500	Recent
Halistrepta	34°N	26°N	27–45	Recent
Halodakra	37°N	4°S	Int–100	Pliocene
Harvella	26°N	4°S	25–70	Miocene
Here	33°N	23°N	5–125	Oligocene
Heterodonax	34°N	4°S	Int	Pleistocene
Hiatella	71°N	54°S	Int–800	Pliocene
Humilaria	60°N	37°N	Int–45	Pliocene
Huxleyia	45°N	33°N	150–600	Pliocene
Hyalopecten	45°N	8°S	3900–4000	Recent
Hyotissa	28°N	1°S	Int–25	Pleistocene
Iphigenia	30°N	3°S	Int–25	Pleistocene
Irus	23°N	34°S	Int–25	Recent
Irusella	38°N	33°N	Int–60	Miocene
Isognomon	34°N	24°S	Int–35	Pliocene
Isorobitella	34°N	23°N	Int–20	Pleistocene
Jouannetia	32°N	7°S	Int	Pliocene
Katadesmia	72°N	54°S	589–3050	Recent
Kellia	60°N	54°S	Int–50	Recent
Kelliella	48°N	6°N	2950–3570	Recent
Kidderia		54°S	Int	Recent
Kingiella		41°S	Int	Recent
Laevicardium	34°N	4°S	Int–180	Recent

Appendix 1 (*Continued*)

Genus	Range		Depth (m)	Epoch*
Lasaea	53°N	52°S	Int–10	Recent
Ledella		33°N	1504	Recent
Leporimetis	30°N	4°S	Int–50	Miocene
Leptomya	19°N	4°S	Int–15	Recent
Lepton	23°N	8°N	?	Recent
Leptopecten	38°N	5°S	Int–250	Miocene
Lima	30°N	2°S	5–110	Pleistocene
Limaria	56°N	43°S	Int–2200	Pleistocene
Limopsis	54°N	56°S	80–3900	Recent
Lioberis	31°N	11°N	Int–30	Recent
Liocyma	71°N	25°N	Int–250	Pliocene
Litharca	10°N	5°S	Int–5	Recent
Lithophaga	33°N	56°S	Int–35	Recent
Lopha	29°N	3°S	1–10	Pliocene
Lophocardium	30°N	6°N	Int–50	Recent
Lucina	60°N	5°S	1–1025	Pliocene
Lucinoma	60°N	54°S	15–750	Miocene
Lunarca	25°N	5°S	20–50	Pliocene
Lyonsia	71°N	54°S	Int–1017	Pliocene
Lyonsiella	52°N	27°S	115–2090	Recent
Lyrodus	38°N	5°S	Int	Recent
Lyropecten	28°N	5°S	Int–200	Pliocene
Macoma	72°N	54°S	Int–1550	Miocene
Mactra	34°N	34°S	Int–30	Pleistocene
Mactrellona	60°N	4°S	Int–110	Pliocene
Malletia	56°N	55°S	25–3900	Recent
Malleus	23°N	9°N	1–50	Recent
Martesia	31°N	2°S	Int	Recent
Megacrenella	60°N	17°N	20–550	Recent
Megapiteria	31°N	4°S	Int–160	Pliocene
Mesodesma	42°S	20°S	Int–5	Recent
Microcardium	28°N	54°S	25–350	Recent
Milneria	37°N	27°N	Int–80	Recent
Miltha	26°N	25°N	55–80	Miocene
Miodontiscus	60°N	33°N	5–2100	Pleistocene
Modiolus	72°N	34°S	Int–3670	Miocene
Montacuta	71°N	64°N	10–40	Recent
Montacutona		33°S	65	Recent
Mullinia	30°N	54°S	Int	Pliocene
Musculus	71°N	35°N	Int–200	Pleistocene
Mya	71°N	37°N	Int–100	Miocene
Myonera	57°N	14°N	1110–3557	Recent
Mysella	71°N	53°S	Int–120	Pliocene
Mytella	31°N	4°S	Int–2	Recent
Mytilimeria	57°N	30°N	Int–45	Recent
Mytilopsis		9°N	Int	Recent
Mytilus	71°N	20°S	Int–120	Pliocene
Nausitora	23°N	12°S	Int–5	Recent
Neaeromya	60°N	1°S	Int–150	Recent
Nemocardium	58°N	28°N	2–150	Pleistocene
Neodavisia	34°S	54°S	100–300	Recent
Netastoma	50°N	54°S	Int–100	Recent
Noetia	30°N	5°S	5–550	Pliocene
Nucinella	28°N	23°N	5–30	Recent
Nucula	72°N	47°S	Int–3900	Pliocene
Nuculana	72°N	51°S	4–3050	Miocene
Nutricola	60°N	27°N	2–120	Recent
Nuttallia	38°N	25°N	Int–5	Pleistocene
Odontogena	60°N	44°N	150–400	Recent
Orobitella	34°N	6°S	Int–120	Pliocene
Ostrea	57°N	8°N	Int–50	Miocene
Pandora	60°N	54°S	2–250	Pliocene
Panomya	71°N	51°N	Int–200	Miocene
Papyridea	31°N	5°S	Int–175	Recent

Appendix 1 (*Continued*)

Genus	Range		Depth (m)	Epoch*
Parapholas	29°N	3°S	Int	Pliocene
Parvamussium	61°N	25°N	15–650	Pliocene
Patinopecten	59°N	36°N	10–200	Pliocene
Pecten	38°N	4°S	10–375	Pleistocene
Pegophysema	30°N	28°N	35–170	Pliocene
Penitella	59°N	26°N	Int	Pliocene
Periglypta	27°N	6°S	Int–5	Pleistocene
Periploma	71°N	4°S	Int–180	Pliocene
Petricola	57°N	45°S	Int–50	Miocene
Pholadidea	28°N	1°S	Int–50	Recent
Phlyctiderma	25°N	3°S	Int–25	Recent
Philobrya	60°N	41°S	Int–50	Pleistocene
Pholas	31°N	42°S	Int	Pleistocene
Pinctada	29°N	5°S	5–30	Pliocene
Pinna	28°N	10°N	Int–5	Pleistocene
Pitar	37°N	55°S	Int–220	Miocene
Placunanomia	26°N	1°S	Int–50	Pliocene
Platomysia	48°N	33°N	Int–20	Recent
Platyodon	55°N	2°S	Int–20	Pliocene
Plectodon	34°N	1°S	20–250	Recent
Pleuromeris		7°N	?	Recent
Plicatula	28°N	1°S	Int–140	Pliocene
Pododesmus	70°N	4°S	Int–90	Miocene
Policordia	55°N	53°S	675–3570	Recent
Polymesoda	25°N	18°S	Int	Pleistocene
Poromya	55°N	48°S	180–3400	Recent
Pristes	33°N	27°N	Int–2	Recent
Propeamussium	43°N	40°S	2650–3300	Recent
Protothaca	60°N	45°S	Int–40	Miocene
Pseudamussium	26°N	7°N	30–600	Recent
Psiloteredo		9°N	Floating	Recent
Pteria	34°N	5°S	5–35	Miocene
Pythinella	23°N	8°N	Int–15	Recent
Raetia	34°N	9°S	2–20	Pliocene
Rangia	31°N	23°N	Int	Recent
Sanguinolaria	31°N	4°S	Int–20	Pliocene
Sarepta	36°N	22°S	3750–5300	Recent
Saturnia	55°N	17°N	37–3700	Recent
Saxicavella	34°N	32°N	7–440	Recent
Saxidomus	60°N	30°N	Int–40	Miocene
Scioberetia		54°S	20	Recent
Semele	60°N	45°S	Int–110	Pliocene
Semelina	30°N	4°N	Int–10	Recent
Semipallium	50°S	43°S	5–10	Recent
Serripes	71°N	47°N	Int–80	Pliocene
Silicula		51°S	223	Recent
Siliqua	72°N	28°N	Int–80	Miocene
Solen	44°N	33°S	Int–40	Miocene
Solemya	58°S	50°S	2–600	Miocene
Sphenia	40°N	54°S	Int–150	Pliocene
Spinula	55°N	32°S	3528–5500	Recent
Spisula	57°S	4°S	Int–95	Pliocene
Spondylus	31°N	5°S	Int–55	Pliocene
Strigilla	30°N	4°S	Int	Recent
Striostrea	23°N	4°S	Int	Pliocene
Strophocardia	27°N	2°S	30–150	Pliocene
Tagelus	43°N	43°S	Int–5	Pliocene
Tapes	52°N	37°N	Int	Recent
Tawera	33°S	54°S	80–150	Recent
Tellidora	31°N	2°S	Int–30	Miocene
Tellidorella	30°N	20°N	25–90	Recent
Tellina	72°N	47°S	Int–440	Pliocene
Temnoconcha	23°N	4°S	5–75	Recent
Teredo	50°N	23°N	Floating	Recent

Appendix 1 (*Continued*)

Genus	Range		Depth (m)	Epoch*
Thracia	61°N	24°S	Int–250	Recent
Thyasira	71°N	53°S	20–350	Pliocene
Tindaria	44°N	54°S	35–4080	Recent
Tiostrea	42°S	30°S	Int	Pleistocene
Tivela	37°N	30°S	Int–75	Pliocene
Trachycardium	37°N	5°S	Int–45	Pliocene
Transenella	28°N	30°S	Int–150	Miocene
Tresus	60°N	28°N	Int–50	Miocene
Trigoniocardia	30°N	4°S	Int–30	Pliocene
Tumbeniconcha	13°N	3°S	20–40	Recent
Turtonia	60°N	40°N	Int	Recent
Uperotus		9°N	90–100	Recent
Ventricolaria	37°N	3°N	10–110	Pliocene
Verticordia	34°N	1°S	15–170	Recent
Vesicomya	53°N	7°N	850–3070	Recent
Xylophaga	55°N	43°S	150–2075	Recent
Zirfaea	70°N	24°N	Int–125	Pliocene

*Earlier occurrence in Western America.

Appendix 2

Bathymetric and geographic ranges of the families of Bivalvia living in the eastern Pacific Ocean.

Family	Range		Depth (m)	Epoch*
Anomiidae	70°N	5°S	Int–130	Miocene
Arcidae	49°N	53°S	Int–4000	Miocene
Astartidae	72°N	(52°S)48°N	Int–500	Pliocene
Bernardinidae	37°N	21°N	Int–100	Pliocene
Cardiidae	71°N	54°S	Int–350	Miocene
Cardiniidae	30°N	20°N	25–10	Recent
Carditidae	71°N	55°S	Int–2200	Pliocene
Chamidae	44°N	5°S	Int–155	Pliocene
Chlamydoconchidae	38°N	27°N	Int–50	Recent
Condylocardiidae	24°N	54°S	Int–150	Pleistocene
Cooperellidae	40°N	25°N	10–45	Pleistocene
Corbiculidae	23°N	18°S	Int	Pleistocene
Corbulidae	37°N	14°S	Int–100	Miocene
Crassatellidae	34°N	5°S	Int–160	Pliocene
Cultellidae	72°N	54°S	Int–100	Miocene
Cuspidariidae	71°N	50°S	10–5400	Recent
Cymiidae	33°S	54°S	Int–250	Recent
Cyrenoididae		9°N	Int–2	Recent
Dimyidae	34°N	29°N	85–1250	Recent
Donacidae	33°N	34°S	Int–25	Pleistocene
Dreissenidae		9°N	Int	Recent
Gaimardiidae	54°S	25°S	Int	Recent
Galeommatidae	31°N	3°S	Int–45	Recent
Gastrochaenidae	28°N	12°S	Int–30	Recent
Glycymerididae	60°N	6°S	Int–250	Pliocene
Hiatellidae	71°N	54°S	Int–800	Miocene
Isognomonidae	34°N	24°S	Int–35	Pliocene
Kelliellidae	48°N	6°N	2950–3600	Recent
Kelliidae	60°N	54°S	Int–400	Pleistocene
Lasaeidae	55°N	52°S	Int–25	Recent
Leptonidae	48°N	33°N	Int–20	Recent
Limidae	56°N	53°S	Int–2200	Pleistocene
Limopsidae	57°N	56°S	80–3900	Recent
Lucinidae	60°N	54°S	Int–1025	Oligocene
Lyonsiidae	71°N	54°S	Int–1020	Recent
Mactridae	60°N	54°S	Int–110	Miocene
Malletiidae	56°N	55°S	25–3250	Recent

Appendix 2 (*Continued*)

Family	Range		Depth (m)	Epoch*
Mesodesmatidae	34°N	42°S	Int–35	Recent
Montacutidae	71°N	54°S	Int–150	Pliocene
Myidae	71°N	54°S	Int–100	Miocene
Mytilidae	72°N	56°S	Int–550	Miocene
Neoleptonidae	34°S	54°S	100–200	Recent
Nucinellidae	45°N	23°N	5–600	Pliocene
Nuculanidae	72°N	51°S	4–3050	Recent
Nuculidae	72°N	47°S	1–3900	Miocene
Ostreidae	60°N	42°S	Int–50	Pliocene
Pandoridae	60°N	54°S	2–250	Pliocene
Pectinidae	72°N	55°S	Int–4000	Miocene
Periplomatidae	71°N	4°S	Int–400	Pliocene
Perrierinidae		42°S	15	Recent
Petricolidae	57°N	45°S	Int–50	Miocene
Philobryidae	60°N	41°S	10–40	Pleistocene
Pholadidae	70°N	54°S	Int–150	Pliocene
Pinnidae	34°N	5°S	Int–30	Pliocene
Placunidae	26°N	1°S	Int–50	Pliocene
Plicatulidae	28°N	1°S	Int–150	Pliocene
Poromyidae	55°N	48°S	150–3400	Recent
Pteriidae	34°N	5°N	5–35	Miocene
Scrobiculariidae	60°N	45°S	Int–4000	Pliocene
Siliculidae	36°N	51°S	220–5300	Recent
Solemyidae	58°N	50°S	2–3000	Miocene
Solenidae	44°N	33°S	Int–40	Miocene
Spheniopsidae	33°N	24°N	5–100	Recent
Spinulidae	55°N	32°S	4000–7230	Recent
Spondylidae	31°N	5°S	Int–55	Pliocene
Sportellidae	31°N	2°S	Int–120	Pliocene
Tellinidae	72°N	54°S	Int–1550	Miocene
Teredinidae	55°N	54°S	Int–100	Recent
Thraciidae	61°N	24°S	Int–250	Pliocene
Thyasiridae	71°N	53°S	Int–2050	Oligocene
Tindariidae	55°N	54°S	30–4080	Recent
Turtoniidae	60°N	9°N	Int	Pleistocene
Ungulinidae	71°N	42°S	Int–150	Oligocene
Veneridae	72°N	54°S	Int–550	Miocene
Verticordiidae	55°N	53°S	15–3600	Recent
Vesicomyidae	53°N	1°N	500–3800	Recent
Vulsellidae	23°N	9°N	1–50	Recent
Xylophagaidae	55°N	43°S	150–2100	Recent
Yoldiidae	72°N	54°S	5–3100	Miocene

*Earliest occurrence in Western America.

Appendix 3

Faunal latitudes calculated from mid-points of distribution of marine intertidal Bivalvia of the eastern Pacific Ocean. *N* = number of species.

Geographical latitude	Faunal latitude	*N*	Geographical latitude	Faunal latitude	*N*	Geographical latitude	Faunal latitude	*N*
60°N	46.8	4	22°N	13.0	56	17°S	21.9	9
59	48.8	5	21	12.8	55	18	22.5	11
58	48.8	5	20	12.6	57	19	22.5	11
57	49.3	6	19	12.4	58	20	24.2	16
56	49.3	6	18	12.3	58	21	24.7	14
55	48.9	8	17	12.2	59	22	25.1	14
54	47.1	8	16	12.0	58	23	25.3	14
53	47.1	8	15	12.0	58	24	25.1	15
52	46.8	9	14	12.0	58	25	25.2	14
51	46.8	9	13	11.9	61	26	25.2	14
50	46.3	10	12	11.6	63	27	25.5	15
49	45.8	11	11	11.3	63	28	25.5	15
48	45.8	11	10	10.8	69	29	25.5	15
47	45.0	11	9	9.5	88	30	26.6	17
46	45.0	11	8	8.4	78	31	28.3	15
45	44.3	10	7	7.9	71	32	28.3	15
44	44.3	10	6	7.6	68	33	30.1	20
43	42.8	12	5	7.5	67	34	30.0	17
42	42.6	12	4	7.5	67	35	30.4	15
41	42.6	12	3	7.4	66	36	30.4	15
40	42.6	12	2	7.3	67	37	31.3	16
39	42.0	11	1	6.7	74	38	32.0	15
38	39.2	13	1°S	6.1N	74	39	32.0	15
37	38.5	15	2	5.2N	65	40	32.0	15
36	36.9	12	3	5.1N	51	41	32.5	16
35	36.4	13	4	3.5N	44	42	34.0	17
34	32.4	15	5	0.8S	30	43	36.7	17
33	32.3	16	6	5.5	17	44	40.9	11
32	29.2	16	7	5.8	14	45	40.9	11
31	26.6	16	8	5.8	14	46	42.2	9
30	25.9	16	9	8.2	15	47	43.1	10
29	24.2	14	10	12.4	12	48	43.1	10
28	21.7	18	11	12.1	12	49	43.1	10
27	20.9	17	12	14.4	14	50	43.9	11
26	17.4	15	13	19.1	10	51	43.9	11
25	14.9	21	14	21.9	9	52	44.6	12
24	14.6	34	15	21.9	9	53	44.7	10
23	15.1	68	16	21.9	9	54	46.2	12

Appendix 4

Faunal latitudes calculated from mid-points of distribution of marine subtidal Bivalvia of the eastern Pacific Ocean. N = number of species.

Geographical latitude	Faunal latitude	N	Geographical latitude	Faunal latitude	N	Geographical latitude	Faunal latitude	N
60°N	59.7	29	22°N	15.4	139	17°S	17.1	3
59	57.6	22	21	15.4	141	18	19.1	4
58	57.7	21	20	15.8	141	19	19.1	4
57	55.1	18	19	14.0	142	20	23.4	7
56	53.5	15	18	14.2	145	21	24.0	6
55	50.0	21	17	14.5	151	22	24.9	6
54	50.1	22	16	13.1	147	23	24.0	6
53	50.4	22	15	13.2	144	24	24.6	7
52	49.1	20	14	13.4	145	25	24.6	7
51	49.3	19	13	13.7	150	26	24.6	7
50	49.3	19	12	13.9	148	27	24.6	7
49	49.3	20	11	12.0	146	28	24.6	7
48	49.3	19	10	12.4	152	29	24.6	7
47	47.1	13	9	12.8	159	30	25.3	8
46	46.6	11	8	11.1	144	31	25.8	6
45	46.6	11	7	10.1	126	32	25.8	6
44	46.6	11	6	10.4	120	33	32.2	14
43	46.6	11	5	10.6	113	34	36.2	6
42	45.9	12	4	10.9	113	35	36.2	6
41	43.4	14	3	10.8	113	36	36.2	6
40	42.3	16	2	10.7	108	37	37.5	7
39	42.3	16	1	9.0	106	38	39.4	6
38	41.0	18	1°S	9.0°N	102	39	39.4	6
37	38.7	25	2	9.4°N	95	40	40.1	5
36	37.6	22	3	9.3°N	76	41	41.4	7
35	36.6	26	4	9.7°N	69	42	42.2	10
34	33.2	38	5	9.5°N	34	43	42.8	9
33	31.2	44	6	3.6°N	11	44	42.8	8
32	29.3	36	7	1.0°S	7	45	43.3	9
31	29.3	36	8	1.0	7	46	44.7	8
30	29.7	37	9	0.5°N	6	47	44.7	8
29	28.8	39	10	4.8°S	4	48	44.7	8
28	24.2	57	11	4.6	4	49	44.7	8
27	22.6	57	12	4.8	4	50	45.5	9
26	21.2	55	13	4.8	4	51	47.6	7
25	20.3	66	14	4.8	4	52	47.6	7
24	18.5	90	15	12.5	2	53	48.9	9
23	17.9	144	16	17.1	3	54	49.0	9
						55	49.6	3

Appendix 5

Bathymetric ranges of some Bivalvia species common to the vicinity of Kuskokwin Bay, Alaska (60°N) and the southern west coast of Vancouver Island, British Columbia (49°N). Depth factor = B.C./Alaska. $\overline{X}$ = mean; SD = standard deviation.

Species	Alaska	B.C.	Depth factors	
			Min.	Max.
Crenella decussata	10–80	5–270	0.5	3.4
Cyclocardia crebricostata	12–50	40–210	3.3	4.2
Cyclocardia ventricosa	20–110	30–100	1.5	1.8
Delectopecten vancouverensis	40–100	80–400	2.0	4.0
Humilaria kennerleyi	Int	5–25	5.0	25.0
Kellia suborbicularis	Int	Int–20	0	20.0
Macoma balthica	Int–10	Int–40	0	4.0
Macoma brota	20–80	10–200	0.5	2.5
Macoma expansa	Int–10	Int–25	0	2.5
Macoma moesta	5–120	10–200	2.0	1.7
Musculus discors	5–50	20–120	4.0	2.4
Musculus niger	15–60	30–80	2.0	1.3
Mya truncata	Int–65	10–100	10.0	1.5
Nucula tenuis	5–89	15–180	5.0	2.0
Nuculana pernula	20–160	40–600	2.0	3.7
Serripes groenlandicus	Int–60	35–70	35.0	1.2
Thyasira goudii	20–100	20–250	1.0	2.5
Tridonta alaskensis	20–80	40–200	2.0	2.5
Yoldia scissurata	15–50	20–120	1.3	2.4
Yoldia thraciaeformis	25–120	30–300	1.2	2.5
$N = 20$		$\overline{X}$	3.92	4.56
		SD	7.69	6.25

Appendix 6

Bathymetric ranges of some Bivalvia species common to the vicinities of Dixon Entrance, British Columbia (54°N) and Cape Mendocino, California (40°N). Depth factor = California/B.C. $\bar{X}$ = mean; SD = standard deviation.

Species	B.C.	California		Depth factors Min.	Max.
Acila castrensis	5–200	18–160		3.6	0.8
Agriodesma saxicola	Int–20	Int–10		0	0.5
Axinopsida serricata	15–120	60–250		4.0	2.1
Bankia setacea	Int–80	Int–40		0	0.5
Cardiomya californica	15–150	45–208		3.0	1.4
Chlamys gigantea	Int–25	Int–50		0	2.0
Chlamys hastata	30–110	10–60		0.3	0.5
Chlamys rubida	15–108	25–200		1.6	1.8
Clinocardium nuttalli	Int–15	Int–50		0	4.0
Compsomyax subdiaphana	9–260	20–400		2.2	1.5
Crenella decussata	10–80	45–90		4.5	1.1
Diplodonta orbella	Int–30	Int–20		0	0.7
Gari californica	Int–15	10–45		10.0	3.0
Glycymeris subobsoleta	10–55	2–45		0.2	0.8
Hiatella arctica	Int–500	Int–320		0	0.6
Kellia suborbicularis	Int–15	Int–20		0	1.3
Lucinoma annulata	20–240	25–162		1.2	0.4
Lyonsia californica	Int–15	Int–90		0	6.0
Macoma carlottensis	5–700	60–944		12.0	1.3
Macoma secta	Int–10	Int–45		0	4.5
Mytilimeria nuttalli	Int–5	Int–45		0	9.0
Mytilus californianus	Int–40	Int–25		0	0.6
Mytilus edulis	Int–2	Int–5		0	2.5
Nemocardium centifilosum	10–50	18–80		1.8	1.6
Nucula tenuis	5–200	30–290		6.0	1.4
Nuculana conceptionis	520–700	470–800		0.9	1.1
Nuculana penderi	45–700	300–600		6.7	0.8
Nutricola tantilla	Int–25	Int–40		0	1.6
Ostrea lurida	Int	int		0	0
Pandora bilirata	20–120	45–90		2.2	0.7
Pandora filosa	25–205	80–225		3.2	1.1
Pandora punctata	5–20	6–45		1.2	2.2
Panope abrupta	Int–70	Int–60		0	0.8
Petricola carditoides	Int–30	Int–72		0	2.4
Philobrya setosa	5–20	Int–40		0.2	2.0
Platyodon cancellatus	Int–10	Int–15		0	1.5
Pododesmus cepio	Int–20	Int–70		0	3.5
Protothaca staminea	Int	Int		0	0
Protothaca tenerrima	Int–5	Int–10		0	0
Psephidia lordi	10–40	30–60		3.0	1.5
Solemya reidi	10–320	16–580		1.6	1.8
Solen sicarius	Int–10	8–40		8.0	4.0
Tellina bodegensis	Int–10	Int–30		0	3.0
Tellina carpenteri	Int–150	Int–250		0	1.7
Tellina modesta	Int–30	Int–50		0	0.9
Turtonia minuta	Int	Int		0	0
Yoldia scissurata	19–150	40–135		2.2	0.9
$N = 47$			$\bar{X}$	1.69	1.77
			SD	2.79	1.64

Appendix 7

Bathymetric ranges of some Bivalvia species common to the vicinities of Manzanillo, Mexico (17°N) and Bahia Solango, Colombia (6°N). Depth factor = Colombia/Mexico. $\bar{X}$ = mean; SD = standard deviation.

Species	Mexico	Colombia	Depth factors	
			Min.	Max.
Adrana exoptata	5–20	8–31	1.6	1.5
Anadara biangulata	15–60	15–65	0	1.1
Anadara mazatlanica	50–100	40–100	0.8	0
Anadara nux	Int–50	Int–45	0	0.9
Anadara tuberculosa	Int	Int	0	0
Arca mutabilis	Int–25	Int–20	0	0.8
Arca pacifica	Int–18	Int–20	0	1.1
Arcopsis solida	Int	Int	0	0
Argopecten purpuratus	20–60	20–40	0	0.7
Atrina maura	3–10	5–10	0	0
Barbatia gradata	Int–40	Int–40	0	0
Barbatia lurida	Int–15	Int–15	0	0
Barbatia reeviana	Int–90	Int–100	0	1.1
Brachidontes adamsianus	Int	Int	0	0
Cardita affinis	Int–5	Int–2	0	0.4
Chama sordida	5–20	2–40	0.4	2.0
Chama venusa	Int–2	Int–1	0	0.5
Chione kellettii	50–60	55–70	1.1	1.2
Corbula nasuta	5–20	5–20	0	0
Crassinella pacifica	Int–85	Int–100	0	1.2
Crassostrea corteziensis	Int	Int	0	0
Ctena mexicana	Int–40	Int–40	0	0
Cyathodonta undulata	Int–60	Int–50	0	0.8
Divalinga eburnea	Int–40	Int–50	0	1.2
Donax californicus	Int–5	Int–10	0	2.0
Donax punctatostriatus	Int–5	Int–5	0	0
Dosinia ponderosa	50–60	50–70	0	1.2
Entodesma pictum	Int–20	Int–15	0	0.7
Felaniella parilis	Int–50	Int–40	0	0.8
Glycymeris inaequalis	Int–20	Int–15	0	1.2
Glycymeris maculata	5–40	10–45	2.0	1.1
Glycymeris multicostata	50–90	60–65	1.2	0.7
Glycymeris strigilata	20–80	15–70	0.7	0.9
Hyotissa solida	Int	Int	0	0
Lithophaga aristata	Int	Int	0	0
Lithophaga plumula	Int	Int	0	0
Lopha angelica	Int–5	Int–5	0	0
Megapitaria aurantiaca	Int–5	Int–10	0	2.0
Modiolus capax	5–40	Int–50	0.2	1.2
Mytella guyanensis	Int	Int	0	0
Noetia reversa	20–70	30–60	0	0.8
Nuculana acrita	45–60	40–65	0.9	1.1
Nuculana elenensis	4–45	10–50	2.5	1.1
Pecten vogdesi	10–160	15–200	1.5	1.2
Pinctada mazatlanica	5–15	5–20	0	1.3
Pitar catharius	10–50	10–60	0	1.2
Pitar lupanaria	Int–20	Int–20	0	0
Pododesmus foliatus	Int–10	Int–10	0	0
Protothaca grata	Int–150	Int–90	0	0.6
Pseudochama panamensis	Int	Int	0	0
Pteria sterna	5–30	5–25	0	0.8
Semele flavescens	Int	Int	0	0
Semele pacifica	Int–20	Int–20	0	0
Spondylus clacifer	2–40	10–50	5.0	1.2
Spondylus princeps	5–20	5–25	0	1.2

Appendix 7 (*Continued*)

Species	Mexico	Columbia		Depth factors	
				Min.	Max.
Strophocardia megastropha	40–120	50–130		1.2	1.1
Tellina meropsis	60–90	60–100		0	1.1
Tellidora burnetti	20–25	20–30		0	1.2
Trachycardium consors	Int–30	Int–40		0	1.3
Transennella modesta	50–70	50–80		0	1.1
$N = 60$			$\overline{X}$	0.32	0.71
			SD	0.83	0.60